Identifying critical foraging thresholds for coral reef fishes

Robert F. Semmler

B.A. – State University of New York, College at Geneseo

M.S. – University of Maryland, College Park

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Supervisors:
Dr. Sally A. Keith (Lancaster University)

Dr. Nicholas A.J. Graham (Lancaster University)

Dr. Nathan J. Sanders (University of Vermont)

Lancaster Environment Centre | Lancaster University

Declaration

This thesis is my own original work and has not been submitted in part or in full for the award of a higher degree elsewhere. Inputs from co-authors has been acknowledged throughout.

- Robert F. Semmler, Apr 2021

Abstract

Foraging behaviour forms the basis for how species interact with one another, affecting not only their own survival, but the overall structure of ecological communities. In this thesis I illustrate the variety of changes in foraging behaviour that are predicted in response to changes in food availability (i.e., bottom-up effects) and evaluate their predictability via optimal foraging theory. I also show the effects of behavioural change and behavioural variation on community structure and ecosystem functional health.

Chapter 2 explores the consistency of predicted optimal foraging responses under decreased food availability. Two evaluated factors showed weak moderating effects on predicted responses: predator taxonomy (mammals are more likely to increase their space-use when food decreases) and prey seasonality (predators with seasonally fluctuating food sources are less likely to increase their space-use).

Then, I evaluate the species-level and community-level outcomes of bottom-up effects, using coral-feeding butterflyfishes and bleaching-induced coral mortality as a model system**.** In **Chapter 3**, I show how bottom-up effects can scale up, from changes in individual behaviour to changes in the structure of interaction networks. In response to substantial coral mortality, coral-feeding fish became consumed increasingly broad diets, weakening their prey preferences. This resulted in significant changes in resource overlap, and substantial rewiring of the consumer-resource interaction network. **Chapter 4** focuses on how specialist and generalist butterflyfishes differ in their foraging behaviour (e.g., patch residence time, bite rate) within low-coral areas, and how these differences might affect their survival.

Lastly in **Chapter 5**, I explored inter- and intraspecific variation in foraging behaviour within coral reef herbivores. I determined that there is significant variation in foraging movement within and across functional groups, highlighting potential complementarity in the scale of their functional delivery. This means together these species may contribute more strongly to grazing than either could alone.

Keywords: *bottom-up effects, optimal foraging theory, dietary preferences, interaction networks, movement*

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Statement of Contributions of Others

This thesis includes collaborations with my supervisors, Sally A. Keith, Nicholas A.J. Graham, and Nathan J. Sanders. It also includes the following additional collaborators: Andrew H. Baird, Simon J. Brandl, Paul J. CaraDonna, James P.W. Robinson, Xin Jing, and David R. Bellwood. Contributions of authors for each data chapter are listed following its Discussion. My supervisors provided guidance, funding, equipment, field assistance, and editorial support.

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1. General Introduction

1.1 Rapid Environmental Change in the Anthropocene

Earth's history has entered a new era dominated by human influence, known now as the Anthropocene (Corlett 2015). Anthropogenic disturbance has rapidly altered natural ecosystems, modifying habitats and altering species compositions (Vitousek et al. 1997, Barnosky et al. 2012). Recent attention has focused on ways for species to respond to cases of human-induced rapid environmental change, through either evolutionary or behavioural means (Sih et al. 2011, Tuomainen and Candolin 2011).

1.2 Behavioural Plasticity

Behavioural responses to anthropogenic disturbance reflect the ability of species to alter their behaviour in varying habitat contexts (i.e., behavioural plasticity). While definitions vary by field, behavioural plasticity generally describes the alteration of behaviour in response to prior experiences or external stimuli (Stamps 2016). In contrast to developmental plasticity, which refers to the expression of different phenotypes as a result of learning (Snell-Rood 2013), the plasticity of foraging behaviour in response to changing conditions is a form of contextual plasticity, wherein external stimuli provide an immediate behavioural response which is typically reversible. This is also commonly referred to as activational plasticity or flexibility (Snell-Rood 2013, van Schaick 2013).

1.3 Bottom-up Effects

Human disturbance can alter numerous aspects of ecological systems, each of which could require a plastic response in foraging behaviour for survival (Sih et al. 2011, Tuomainen and Candolin

2011). For a given species, disturbance may result in changes in its population size, the population size of its predators (top-down effects), the availability of its food resources (bottom-up effects), or changes in its physical habitat (Wilson et al. 2020). In particular, bottom-up effects are likely to result in wider ecosystem change, because resulting changes in foraging behaviour or diet can alter consumer-resource interactions, ultimately affecting the structure of food webs (Wong and Candolin 2015). Human disturbance can result in sharp decreases in food availability, which often stem from habitat destruction (e.g., deforestation for frugivorous primates [Pangau-Adam 2015], coral reef bleaching for corallivorous fishes [Wilson et al. 2014]). Human influence can also increase the abundance of food items, such as through anthropogenic food subsidies (Quinn and Whisson et al. 2005, Merkle et al. 2013), or through increases in the vulnerability of food items as a result of human activity (Ramsay et al. 1998, Devereaux et al. 2006).

1.4 Optimal Foraging Theory

Many examples of activational plasticity in foraging behaviour parallel predictions established decades prior within optimal foraging theory. Optimality models have set the basis for our expectations of how foraging species interact with their environment (Stephens and Krebs 1986). These predict optimal foraging patterns by setting a currency (typically long-term net energy gain) and mathematically determining the foraging patterns which maximize it (Houston and McNamara 2014). Specifically, in the context of this thesis, three important optimality models predict changes in foraging behaviour that could result from changes in food availability.

First, models of optimal territory size determine a territory which provides a maximum net energy benefit, considering the costs and benefits of territory defense (Brown 1964). Benefits are typically determined as a function of the distribution of food items, and their rate of replenishment, whereas

costs are influenced by the energetic expense involved in territory defense from intruders (Adams 2001). These models predict that when food availability decreases, foragers should expand their territory in search of food (**see Chapter 2**, Dill 1978, Hixon 1980, Ford 1983).

Second, the optimal diet model (Emlen 1966) seeks to identify a diet which maximizes long-term energy gain, assessing the energetic benefit of each potential food item, based on its energy value, abundance within the environment and necessary handling time (Charnov 1976a). It considers each encounter with a food item sequentially, so the forager has a binary choice between consuming the food item in question or moving on in search of another. In this way, the food item will be consumed if it's energetic benefit is greater than those it is likely to find otherwise. Because of this, the model predicts a strict diet, where each food item is either always consumed when encountered, or always ignored (i.e., the "zero-one rule", Pulliam 1974). However, partial prey preferences are common in natural systems as food items may contain different nutrients a forager must consume or may produce toxins that can cause harm in large amounts (Pulliam 1975, Hirakawa 1995). When food availability is low, the optimal diet model predicts that foragers will expand their diets in response (**see Chapter 3**, Emlen 1966).

Lastly, the marginal value theorem (also known as the Patch Model), defines the conditions for optimal patch occupancy, attempting to maximize long term energy gain (Charnov 1976b). It too, considers each patch sequentially, comparing the energetic benefit of remaining in a given patch against the opportunity cost of moving to a new one. A forager will remain in a patch as long as the instantaneous energy gain within that patch is greater than the average rate of energy gain within the nearby environment. Because of this, the marginal value theorem predicts that residence times within a given patch type will be longer when surrounded by low-quality habitat than when

surrounded by high-quality habitat (Krebs et al. 1974). It can then be predicted that when food availability decreases, foragers should have longer patch residence times (**see Chapter 4**).

However, tests of optimal foraging theory have had mixed results (Sih and Christensen 2001), and behavioural responses to changing food availability can vary from system to system, dependent on a variety of context-dependent factors (Caro 2007, Gordon 2011). As such, a better understanding of these factors and constraints on theoretical responses is needed.

1.5 Coral Reef Ecosystems

Coral reefs are incredibly diverse ecosystems, owing much of this diversity to their structural complexity and wide variety of microhabitats (Reaka-Kudla 1997, Graham and Nash 2013). Tropical reefs cover less than 1% of the ocean floor (Spalding et al. 2001), but are estimated to contain one-quarter to one-third of marine species (Plaisance et al. 2011). However, estimates of species richness vary substantially, as much of this diversity is within understudied groups (i.e., invertebrates, Reaka-Kudla 1997, Fisher et al. 2015, Hoeksema 2017), or organisms that are cryptic in nature (Brandl et al. 2018), evading detection within popular visual sampling protocols (Rogers et al. 1983, English et al. 1997). The wide variety of organisms that make their homes within coral reefs owe their survival to the symbiotic relationship between corals and photosynthetic algae that live inside their tissues (*Symbiodinium* among others, Muscatine 1967, Muscatine and Cernichiari 1969). In exchange for protection inside coral tissues, the photosynthetic products of these algae can provide up to 100% of a coral's daily energy demands (Muscatine et al. 1981, Grottoli et al. 2006). This energy source fuels their reproduction and supports the continued buildup of reef structure through growth and calcification.

1.5.1 Coral reef bleaching

Coral reefs also face extreme threats under anthropogenic change from a number of stressors including fishing, eutrophication, and disease (Hughes et al. 2017, Ban et al. 2014, Harborne et al. 2017). Of these, one of the most notable threats to reef health is climate change and the devastating effects of thermal bleaching events. Under extreme thermal stress, corals will bleach, shedding their symbiotic algae and risking starvation (Brown 1997, Lesser 2010). Bleaching events can result in widescale coral mortality and, in combination with other stressors, result in phase shifts to algal dominated states (Bruno et al. 2009, Norström et al. 2009). Bleaching-induced mortality can cause rapid population declines and extirpations among reef fishes, particularly among those species which rely on coral for food or shelter (Wilson et al. 2014). This unequal turnover of species can reshape fish communities, leading to biotic and functional homogenization (Richardson et al. 2018).

As a result of ocean warming, coral bleaching events are now five times as common as they were in the early 1980s (Hughes et al. 2018). While reefs can recover from bleaching, this can be a lengthy process, requiring 7-29 years without additional disturbance (Gouezo et al. 2019, Robinson et al. 2019). However, as a result of their increasing frequency, the average window for a given reef to recover between bleaching events has shortened to just six years (Hughes et al. 2018). With continued increases in global ocean temperature, the future of coral reefs will be defined by the relative ability of their component species to persist through bleaching events. For fish populations, this will depend on their behavioural response to bleaching events, which may or may not be adaptive (Coppock et al. 2015, Boström-Einarsson et al. 2018). Because of this, bleaching-induced coral mortality events provide a valuable opportunity to evaluate bottom-up effects on foraging behaviour, through their effects on coral-feeding fishes.

1.5.2 Coral reef ecosystem functioning

The condition of coral habitats is guided by a set of eight core functional processes, working in complementary pairs (Brandl et al. 2019). *Calcium carbonate production* (1) by corals determines the accretion of reef structure and is countered with *bioerosion* (2). *Primary production* (3) by photosynthetic algae and cyanobacteria is countered with *herbivory* (4). *Secondary production* (5) of fish and invertebrate biomass is countered with *predation* (6). Lastly, *nutrient release* (7) is countered with *nutrient uptake* (8). Effective management of coral reefs requires maintenance and balance of these processes, to ensure reefs do not transition into undesirable states (Bruno et al. 2009, Norström et al. 2009). And doing so requires a full understanding of the populations that contribute to these essential functions, the complementarity of their actions, and their future within disturbed reefs (Nyström 2006, Burkepile and Hay 2011, Brandl et al. 2019). Most notably, management efforts have focused particularly on maintaining sufficient herbivory to counter algal growth and prevent phase shifts to algal dominated states (Green and Bellwood 2009).

1.5.3 Corallivores, corallivory, and its functional role

Corallivory is the direct consumption of live coral, and some corallivores can contribute to the essential function of bioerosion (Rice et al. 2019). However, the mechanics of coral consumption (and their effects on coral growth and survival) are varied and complex (Rotjan and Lewis 2008, Konow et al. 2017). Some species scrape or excavate corals to consume both coral tissue and the underlying coral skeleton (e.g., parrotfishes, Bellwood and Choat 1990), whereas others focus on direct removal of coral tissue (i.e., browsers, Hiatt & Strasburg 1960) or coral mucus. In particular, this thesis will focus on the feeding behaviour of coral-feeding butterflyfishes (Genus: *Chaetodon*), which (though some species occasionally consume coral skeleton, Motta 1988) are primarily browsers, and feed directly on coral polyps.

Due to their reliance on large quantities of healthy coral, coral-feeding butterflyfishes serve as a valuable "indicator" of healthy reef condition (Hourigan et al. 1988), with species expected to alter their behaviour and abundance in response to poor reef health (Crosby and Reese 1996, 2005). and are often among the first and most-strongly affected by coral reef disturbances, frequently declining in population following coral mortality (Wilson et al. 2014). They also can face a variety of sublethal effects, showing reduced body condition when coral cover is low (Pratchett et al. 2004). Following examples from other groups (dameselfishes), it's possible that poor body condition could affect their growth, reproduction, or behaviour (Jones 1986, Kerrigan 1997). Given the clear link between coral abundance and the health of coral-feeding butterflyfishes, and the rapid nature of their population declines following bleaching, they serve as a valuable model system for the study of bottom-up effects.

While originally thought to have limited impacts on coral communities (Harmelin-Vivien and Bouchon-Navaro 1983, Hixon 1997), the combined consumption of butterflyfishes can add up. Over the course of a year, butterflyfishes can consume 9-14% of the live tissue on a reef, posing a substantial energetic strain (Cole et al. 2011, Cole et al. 2012), and their continued feeding has major implications for coral recovery after bleaching. Additionally, recent research efforts have connected coral consumption by butterflyfishes with both the reuptake of coral symbionts (Grupstra et al. 2021), and the spread of coral disease (Aeby and Santavy 2006, Chong-Seng et al. 2011, Noonan and Childress 2020), and both of these processes could play a major role in reef health.

1.5.4 Herbivores, herbivory, and its functional role

Herbivory is an essential function that protects corals against overgrowth by algae and is traditionally broken down into four functional groupings (Bellwood et al. 2004, Nyström 2006,

Green and Bellwood 2009). Browsers (1) consume macroalgae, preventing it from overshading live corals. Grazers (2) consume epilithic algal turf, limiting the establishment of macroalgal patches. Scrapers and bioeroders (3 + 4), consume algal turf as well, but also take with it a varying portion of the reef substratum, scraping the top layer, or substantially excavating live and dead corals, respectively. However, these broad groupings can mask a variety of important differences between species that may serve as sources of complementarity in their functional roles, such as differences in microhabitat use (Fox and Bellwood 2013, Brandl and Bellwood 2014, Adam et al. 2018, Puk et al. 2020).

Without sufficient herbivory, and without redundancy within important herbivore groups, reefs can shift to undesirable algal dominated states (Bruno et al. 2009, Norström et al. 2009). For example, due to historical overfishing in the Caribbean, the sea urchin *Diadema antillarum* served as the keystone grazer on Caribbean reefs (Hughes 1994). However, after a disease outbreak among urchins drove down their populations (Hughes et al. 1985, Lessios 2003), the lack of grazing pressure (in addition to the stresses of bleaching and hurricane damage) led to phase shift to a macroalgal state.

In recent years, management efforts have focused on maintaining herbivore populations to prevent algal overgrowth (Green and Bellwood 2009), with efforts focused on maintaining a diverse herbivore community that is resilient to individual species losses (Adam et al. 2015a,b). This means ensuring that the different functional groupings of herbivores are maintained with sufficient redundancy, and with sufficient coverage of the complementary roles and behavioural patterns that exist within them.

1.6 Thesis Outline and Objectives

In this thesis, I aim to evaluate the variety of behavioural responses that can be predicted from bottom-up habitat disturbance, as well as their predictability via optimal foraging theory. I also seek to better understand the effects of behavioural change and behavioural variation on community structure and ecosystem functional health. This thesis addresses the following questions:

1) How consistently do natural populations follow predictions of optimal foraging theory in response to changes in food availability? Are there any context-specific factors which decrease the likelihood of the predicted response?
2) How do changes in food availability affect dietary breadth and the strength of dietary preferences, and how can this scale up to affect species interaction networks?
3) How do changes in food availability affect foraging traits (patch residence, bite rate, etc.), and how does this vary between specialists and generalists?
4) How does foraging movement behaviour vary among coral reef herbivores? Is there substantial complementarity in foraging behaviour within traditional functional groups?

First, I conduct a meta-analysis of published research articles detailing foraging responses to changing food availability (**Chapter 2**). Then, I evaluate a mass coral bleaching event which occurred in Iriomote, Japan and its effects on the behaviour of coral-feeding butterflyfishes (Genus: *Chaetodon)*. I determine individual behavioural change in dietary breadth and the strength of dietary preferences and evaluate how this scales-up to produce structural change within fish networks (**Chapter 3**). Following this, I further evaluate individual effects of the bleaching event

on foraging behaviour, with particular attention to changes in physical foraging traits (bite rate, patch residence time, etc.) among specialist and generalist coral-feeders (**Chapter 4**). I also evaluate behavioural diversity among reef herbivores (Genera: *Scarus and Siganus)* on the Great Barrier Reef, Australia (**Chapter 5**).

Each data chapter within this thesis (**Chapters 2-5**) was written for publication. **Chapter 2** is in preparation for submission to *Biological Reviews*. **Chapter 3** is in preparation for submission to *Journal of Animal Ecology*. **Chapter 4** is also in preparation for submission to *Journal of Animal Ecology*. Lastly, **Chapter 5** is published in *Ecology & Evolution.*

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2. Factors limiting the likelihood of optimal space-use responses with changing food availability

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Robert F. Semmler[1], Nicholas A.J. Graham[1], Nathan J. Sanders[2], Sally A. Keith[1]

[1]Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, UK

[2]University of Vermont, Burlington, VT, 05405, USA

2.1 Abstract

Anthropogenic influences can alter foraging behaviour in a number of ways. One of the most striking of these is a change in behaviour as a result of altered food availability (i.e., bottom-up effects). Predicting bottom-up effects is an appealing prospect for management purposes, but behavioural responses to disturbance are known to be highly context-dependent, and relatively little is known about potential constraints on changes to foraging behaviour. Optimal foraging theory predicts a number of responses when animals face a decrease in food availability, including changes in 1) home range, 2) feeding distance, and 3) aggressive behaviour. Through a systematic review of published field studies, we evaluated the degree to which forager populations display predicted theoretical responses and investigate possible factors which may result in a response inconsistent with predictions. We did so through direct calculation of effect sizes for changes in food availability and changes in behaviour within the study populations. Overall, we found that populations consistently showed a negative association between changes in food availability and changes in feeding distance, but responses were less consistent for changes in home range. We found weak moderating effects for predator taxonomy and prey seasonality, with predicted responses most likely to occur for mammals and for predators targeting non-seasonal food sources.

Keywords: *food availability, optimal foraging theory, conservation-behaviour, space-use, aggression*

2.2 Introduction

Anthropogenic disturbance events have rapidly altered the habitats of species globally (Vitousek et al. 1997, Wong and Candolin 2015). As a result, a variety of behavioural responses have been observed, which may be adaptive, promoting survival, or maladaptive, leading to potential declines and extirpations (Sih et al. 2011, Tuomainen and Candolin 2011). How species respond to disturbance will not only affect their ability to withstand these events, but also the degree to which interventions and management strategies are effective in protecting them (Berger-Tal et al. 2011). Therefore, building the knowledge necessary to predict, or effectively manage for, behavioural responses to disturbance is an appealing prospect. However, the field of conservation behaviour is still in its infancy, and expectations of consistent responses are poorly defined (Caro 2007, Angeloni et al. 2008, Tuomainen and Candolin 2011, Berger-Tal and Saltz 2016).

One framework that has provided valuable insight into forager responses over the past seven decades is optimal foraging theory (MacArthur and Pianka 1966, Stephens and Krebs 1986). In this time, these models have evolved in a variety of ways, tackling issues such as incomplete information / learning (e.g. Stephens 1987, Dall et al. 2005, Dunlap and Stephens 2012), variable handling times (e.g Sih 1980, Anderson 1984), and multiple currencies (e.g Simpson and Raubenheimer 1993, Simpson et al. 2004). Additionally, a variety of potential caveats and constraints have been posed as to why systems may not seem to follow optimal foraging predictions. One such example is the optimal diet model (Emlen 1966), which predicts an energy-maximizing diet considering each food item's energetic value, availability within the environment, and necessary handling time. This model has been observed to be less effective at predicting diets in studies where foragers target mobile prey (Sih and Christensen 2001). This is expected to be a result of variations in prey vulnerability, which are difficult to account for, and will have critical

effects on encounter and capture rates. Similarly, dietary expansion events predicted under the optimal diet model may not be realized if disturbance also reduces the diversity of food items available to foragers (e.g. Haley et al. 2011, Folks et al. 2014). Nonetheless, these theoretical bases remain tractable in a variety of circumstances and have continued to predict recent natural phenomena where they can be applied appropriately (e.g. Watanabe et al. 2014).

One important pathway for behavioural change in disturbed communities is the effect disturbances can have on the amount of food available to foraging animals (bottom-up effects, Wilson et al. 2020). Examples of anthropogenic disturbance causing a reduction in food availability are numerous, ranging from deforestation and its effects on frugivorous primates (Heiduck 2002, Pangau-Adam 2015) to coral reef bleaching and its effects on coral-feeding fishes (Wilson et al. 2014, Keith et al. 2018, See Chapters 3+4). Similarly, anthropogenic disturbance can provide sudden increases in food supply, such as anthropogenic food subsidies in urban environments (Beckmann and Berger 2003, Prange et al. 2004, Quinn and Whisson et al. 2005, Merkle et al. 2013), or temporary increases in vulnerability of food items due to human activity (Garthe et al. 1996, Ramsay et al. 1998, Vickery et al. 2001, Devereaux et al. 2006).

Predicting bottom-up effects on animal behaviour is complex, and to do so reliably, we need a better understanding of the constraints that may prevent particular populations from following optimal foraging predictions. Meta-analysis and systematic review methods serve as an important tool to sort through context-specific behavioural outcomes to better understand their causes or predictors (Koricheva and Gurevitch 2014, Berger-Tal et al. 2019). Prior reviews have tested the predictive quality of a variety of optimal foraging models (Stephens and Krebs 1986, Sih and Christensen 2001). And while results have been mixed, common factors tested against predictive quality include study type (lab vs. field), taxonomy (endothermic vertebrates vs. ectothermic

vertebrates vs. invertebrates) and prey mobility. Other factors tested specifically against optimal home range responses include body mass, sex, and latitude (Gompper and Gittleman 1991, McLoughlin and Ferguson 2000, Ofstad et al. 2016).

In addition to these direct tests, there are a variety of other field studies on individual populations responding to either natural variations, or experimental manipulation of food availability (e.g., Marshall and Cooper 2004, Loveridge et al. 2009, Chandler et al. 2016). Though these studies are often not planned as tests of optimal foraging theory, and may not hold the same assumptions, together they could hold valuable information on context-specific outcomes, and constraints to optimal foraging behaviour. To our knowledge there is one review to date which collects these types of studies to explicitly test the effects of food availability on any one of these responses (home range size, Adams 2001), though these were only assessed qualitatively, and no potential constraints were directly tested. In the time since this publication there has been an abundance of new studies on these relationships, and in addition, data extraction tools have come into greater popularity in evidence synthesis to extract relevant information directly from study figures, where it is not reported in the text (Tummers 2006, Flower et. 2016, Lajeunesse 2016). This provides a unique opportunity to use published field research to test the consistency of predicted optimal foraging responses, and quantitatively assess the strength of any potential constraints on foraging behaviour.

In response to changes in food availability, optimal foraging theory predicts foraging animals should change three important foraging traits (in addition to dietary changes mentioned above): home range, feeding distance, and aggression. When food availability decreases, so will the potential food intake within a given home range. In response, foragers should expand their home ranges in search of food (Dill 1978, Hixon 1980, Ford 1983). Similarly, foragers are predicted to

travel further distances between feeding events, or further distances from a central place (Brown and Orians 1970, Covich 1976), hereafter referred to as "feeding distance". Aggressive behaviour, on the other hand, provides an optimal energetic benefit to a forager at intermediate levels of food availability (Peiman and Robinson 2010), and may be wasteful when there is more food than needed, or when food resources are too limited to be particularly valuable to defend (Brown 1964, Enquist and Leimar 1987). Because of this (and in contrast to the directional relationships for home range / feeding distance), foragers may either increase or decrease aggression in response to food reduction.

Additionally, a number of factors evaluated in the reviews above could act as constraints, modulating the effects of the predicted optimal foraging responses. **Predator taxon** could influence responses, as large taxonomic groups can differ in sensory and neural complexity (vertebrates vs. invertebrates) or energy demands (endotherms vs. ectotherms) impacting their ability to make informed or energy-maximizing foraging decisions (Sih and Christensen 2001). Just as the stochastic attack and capture probabilities of **mobile prey** can influence dietary responses, these could affect other responses to food availability, by altering the ability of a predator to assess habitat quality (Sih and Christensen 2001). Foragers that experience **seasonal fluctuations in food availability** could have evolved alternate adaptive behaviour such as hibernation, preventing predicted responses (Geiser 1998, Humphries et al. 2003). **Social foragers** may have increasingly complex decision-making processes (Fernandez-Juricic et al. 2004), with multiple individuals tracking resource quality and sharing that information among the group (Barta and Szep 1992, Day et al. 2001, Dechaume-Moncharmont et al. 2005). Additionally, a variety of disturbances to food availability may be patchy in nature, the scale of which may affect a solitary forager differently than a group with a larger shared territory. Lastly, individuals with larger **body**

sizes may be more likely to make informed or energy-maximizing foraging decisions due to their generally larger brains (Font et al. 2019) or greater energy demands. If any of these factors are identified as constraints, they could negatively impact the ability to apply these predictions broadly across systems.

Here, we test the degree to which natural responses of foraging animals follow predictions from optimal foraging theory using a meta-analysis approach. We used quantitative data from 49 field studies, contained within 38 published articles across a variety of systems. We directly compare effect sizes of change in food availability against effect sizes of change in one of three related traits: home range size, feeding distance, and aggressive behaviour. We also sought to determine the extent to which each of the three optimal foraging responses have been studied, and how evenly studies are spread across different taxonomic groups. Specifically, we tested whether there was a consistent negative association between changes in food availability, and changes in home range / feeding distance, as predicted by optimal foraging theory. In addition, we expected a mixed association between changes in food availability, and changes in aggressive behaviour (a mixture of positive and negative responses). We also seek to explore potential constraints that may limit the degree to which systems follow the predictions of foraging theory. Specifically, weaker space-use responses (changes in home range / feeding distance) may be seen among ectothermic predators, predators targeting mobile prey, predators targeting seasonal prey, social foragers, or small-bodied predators.

2.3 Methods

2.3.1 Data collation

We performed a search of the ISI Web of Science for relevant studies. Our evidence search followed a PICO (Population / Intervention / Control / Outcome) framework with the overarching study question: how do foraging animals (P) alter their behaviour in response to differences in food availability (I/C); specifically, how do differences in food availability affect their home range, feeding distances, and aggressive behaviour (O) (Booth 2004, Higgins and Green 2011, Bayliss and Beyer 2015)? This framework guided the development of search terms, generating a set of terms focusing on each of the three research questions (feeding distance [1], home range [2], aggression [3]) and a set that focused on the intervention/control (food availability [4]) (Heneghan and Badenoch 2002). Search terms utilized are listed in Table 2.1.

To identify papers which draw a connection between food availability and behaviour, each search for a specific behaviour (1-3) was combined with the search for all terms related to resource availability (4) to limit solely to papers that included both a behaviour term and a term of resource availability. To ensure broad coverage of the various terms that could be used to describe the desired behaviours across multiple fields, we scanned the table of contents of related journals for comparable terms that may have been missed. Tables of contents for all 2017 issues of the journals American Naturalist, Journal of Ethology, and Behavioral Ecology were scanned. Terms added to the searches as a result included: (3) “territorial defense”, “resource defense”, “agonism”, (4) “resource depletion”, “resource deterioration”.

We extracted all necessary article info (title, abstract, year, journal) to find appropriate data sources. Titles, abstracts, and full texts were read for relevance in three stages, according to the

Response Variable	Search	Resulting Papers
1) Feeding Distance	TS=(forag* NEAR/2 distance* OR feed* NEAR/2 distance* OR interforay OR intraforay)	1,504
2) Home Range	TS=(foraging NEAR/1 area* OR foraging NEAR/1 range* OR feeding NEAR/1 area* OR feeding NEAR/1 range* OR "home range")	15,458 / 10,909
3) Aggression	TS=(territoriality OR territorial NEAR/1 behavior OR aggressive NEAR/1 behavior OR aggression OR agonism OR territorial NEAR/1 defen?e* OR resource* NEAR/1 defen?e* OR aggressive NEAR/1 interaction*)	80,722
4) Resource Availability	TS=(resource* NEAR/1 availa* OR food* NEAR/1 availa* OR habitat* NEAR/1 condition* OR resource* NEAR/1 condition* OR resource* NEAR/1 variab* OR habitat* NEAR/1 quality OR resource* NEAR/1 deplet* OR resource* NEAR/1 deterior* OR prey NEAR/1 availa* OR resource* NEAR/1 unavaila* OR prey NEAR/1 condition*)	69,334
A) Feeding Distance + Resource Availability	#1 AND #4	126
B) Home Range + Resource Availability	#2 AND #4	1,355 (300 Scanned)
C) Aggression + Resource Availability	#3 AND #4	753 (300 Scanned)

Table 2.1 Search terms used to identify studies connecting one of the three desired behaviours to the level of food availability, as well as the number of papers which resulted from each search. The search for the given behaviour (1-3) was combined with the search for food availability (4) to limit to papers mentioning both (A-C).

following criteria (see PRISMA flow diagram, Fig. 2.1). In the first level of refinement, articles were eliminated if their title did not refer to the ecology of a foraging animal or animals. At the second stage, articles were selected if the abstract mentioned a relationship between the given foraging trait (home range, feeding distance, aggression) and resource availability, or both were

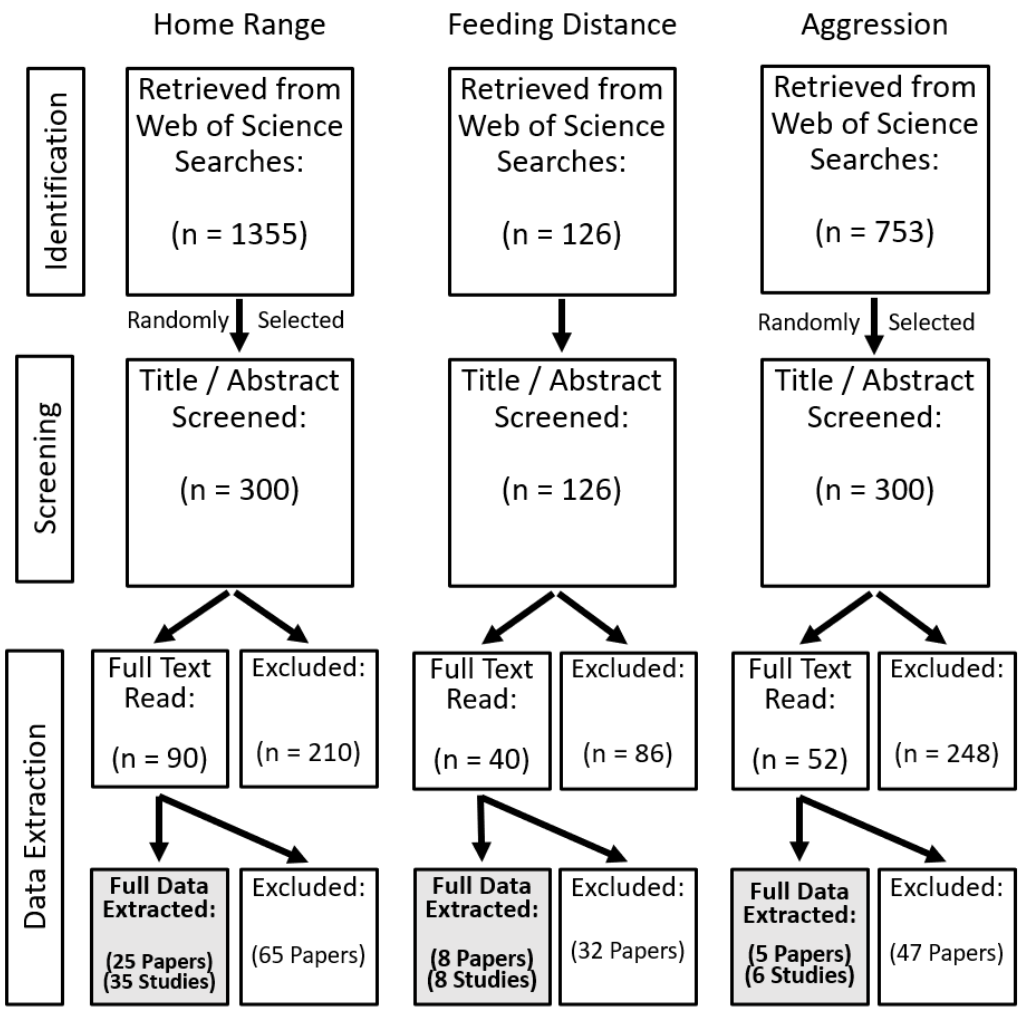

Figure 2.1 Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram of systematic review search methods.

mentioned in some way. Due to the large number of papers resulting from some of the Boolean searches (1,355 in the case of home range), we randomly shuffled the order of the papers and then selected the first 300 abstracts for each of three traits. At the final stage, full texts for remaining articles were scanned and articles were selected for quantitative analysis if they recorded both a quantitative measure of one of the above behaviours, and a measure of resource availability, at multiple points in time or in multiple locations. Articles were then categorized as

to whether the authors observed a positive relationship, a negative one, observed no relationship, or the relationship was untested.

2.3.2 Extracting behavioural response data

Desired quantitative measurements for response behaviours included: (1) mean distance between feeding events (m), distance travelled from a central place (m), (2) home range (Ha), and (3) aggressive interactions per minute. Quantitative measurements for resource availability included: % cover of food resource, density of food resource (# m^{-2}). Measurements were extracted from the full text for use in quantitative analyses. Designations were also made between studies measuring behaviours before and after a change in resources, and studies measuring behaviours in varying habitats. However, both were included in the quantitative analysis here if metrics used were comparable. For those articles which directly reported a mean and variance for both the food availability and the behaviour, these were extracted from the text and used to calculate effect sizes (Cohen's d). Cohen's d values were then converted to standardized correlation values (r) for ease of interpretation and model fitting. For some articles, means and variances were not given directly but were estimated from plots and error bars using the program Datathief III, which reliably extracts data for meta-analysis purposes (Tummers 2006, Flower et al. 2016). For articles which gave scatterplots of the given behaviour against food availability, values were pulled out with Datathief III, points were split evenly into "Low Food" and "High Food" sets and their means and variances were calculated manually.

This analysis focused specifically on field studies for two reasons. Firstly, though both field and laboratory studies have been relatively equivalent in following predictions from optimal foraging theory, field studies should better reflect the natural conditions which can pose difficulty in predicting behavioural response (Stephens and Krebs 1986, Sih and Christensen 2001). Secondly,

the nature of most laboratory-based food availability experiments did not lend itself to this specific quantitative analysis, as exact quantities of food were portioned to subjects, preventing us from calculating an effect size for these differences.

2.3.3 Extracting explanatory variables

For all studies with extractable data we also determined a set of criteria related to these systemic factors which could in some way influence the behavioural response seen:

1) **Predator Type**: Due to the paucity of useable studies on invertebrates, we were unable to directly compare between vertebrates and invertebrates. Instead we compared ectotherms (vertebrate and invertebrate) against two populous categories of endotherms (mammals, and birds)

2) **Prey Mobility**: We divide prey mobility into three categories, particularly because a variety of foragers consume both mobile and immobile prey: mobile, immobile, and mixed / partially mobile.

3) **Prey Seasonality**: For each study we assessed whether the density of food items for the forager in question did, or did not follow a strong seasonal fluctuation, for example the difference between wet and dry seasons for a folivore or frugivore.

4) **Predator Social Organization:** We divided social organization into three categories: solitary foragers, group foragers, and those with mixed strategies / transient foraging groups.

5) **Body Size**: Lastly, we assessed body size of the forager in question quantitatively, extracting the mean body mass (in kg) of an adult from relevant sources.

2.3.4 Overview of studies

To better understand what is known and evaluate potential knowledge gaps, we first investigated the overall coverage of studies investigating these patterns. For each of the three traits, we determined the number of studies which made a connection between this trait with food availability. We also determined the number of studies which reported data that could be extracted for our purposes. However, as only a subset of the search results for some traits (Area + Aggression) were scanned, exact comparisons of numbers of studies cannot be made between traits. We also investigated the spread of these studies across broad taxonomic categories (e.g., birds, mammals, fish), as well as the accumulation of these studies over time.

2.3.5 Consistency of optimal foraging responses

A secondary goal was to evaluate the consistency of predicted optimal foraging responses. Following a vote-counting approach, we pulled out each study with extractable data and categorized whether these data represented a positive or negative relationship between the given trait and food availability. We then calculated the mean behavioural response for each trait, as well as the standard effect size of these values from zero.

2.3.6 Evaluating potential constraints

Lastly, we wished to determine which, if any, of the factors mentioned above had an effect on the likelihood that foragers followed the predicted response. We did so through meta-analysis, directly comparing effect sizes of the selected studies. Given the nature of this study and the limited data which could be extracted, natural model averaging was the preferred approach to quantify the strength of the potential explanatory variables. While other studies have employed a sum of weights method to compare predictor strength, this has been shown to produce variable results and

can be an unreliable approach, especially with smaller datasets (Galipaud 2014, Galipaud et al. 2017). Instead, a more reliable approach is comparing model averaged parameter estimates. Specifically, natural model averaging involves generating an averaged parameter estimate for each predictor, based only on the candidate models which included that estimate. It is preferred when seeking to quantify the absolute effect size of each parameter (Galipaud et al. 2017). The alternative, full model averaging, is preferred in cases where the goal is to select an ideal set of predictors for a parsimonious model. For our purposes natural averaging was preferred — given the limited number of studies with fully applicable data and the great degree of variety in experimental setups, even a weak effect for these factors could prove informative.

All models utilized were gamma GLMMs (generalized linear mixed models) with log link functions. While the response variable, scaling from 0 to 1 would seem to be well-suited to a beta model, fitting such a model led to substantial overdispersion (disp index = ~6). As some papers ran multiple studies on separate species, or multiple studies within different populations / social groups of the same species, there was dependency among studies within the same paper. To account for this dependency, we used the identity of each paper as a random intercept effect. Model averaging was performed via the dredge function in package "MuMIn" (Barton 2009) in R (R Core Team, 2019). This was performed on a subset of the extracted data, including only studies on changes in feeding distance and home range size. As aggressive behaviour was predicted to show a variable response with changing food availability, rather than a consistent negative relationship, it could not reliably be included in the same model as the other two traits. Natural model averaging was performed on a subset of models within 3 ΔAICc of the best model, as these should function essentially as well (Richards 2005, Symonds and Moussali 2011).

2.4 Results

2.4.1 Overview of studies

Initial Boolean searches resulted in 126 papers for feeding distance, 1355 for home range, and 726 for aggression. Resulting papers showed interesting taxonomic divides, with mammals and birds together making up the majority (Fig. 2.2), however, this varied between the three traits evaluated. Specifically, we report these divides among abstracts which drew a potential connection between food availability and the given trait, whether or not they found this to be true in their system. There has been a steady accumulation of studies fitting these criteria over time (Fig. 2.3). Abstracts which drew a connection between food availability and home range were heavily dominated by mammals (73.0%), with most others focused on birds (20.0%) (Fig. 2.2). Abstracts that connected food availability to feeding distances were primarily focused on birds (48.4%), with most other studies assessing either insects (22.6%) or mammals (19.4%). Abstracts that connected food availability to aggression were primarily on mammals (47.4%) with most others assessing birds (26.3%) or insects (14.0%). While there are numerous papers which connect or attribute behavioural change to changes in food availability, the strict data requirements of this study led to only a few studies which could be fully used in the meta-analysis. From the 126 abstracts which were read for feeding distance, eight studies were selected for data extraction. From the 300 which were read for home range, 35 studies were selected. And from the 300 which were read for aggression, six were selected (see PRISMA flow diagram, Fig. 2.1). A full listing of all papers used in quantitative analyses is listed in Table S2.1.

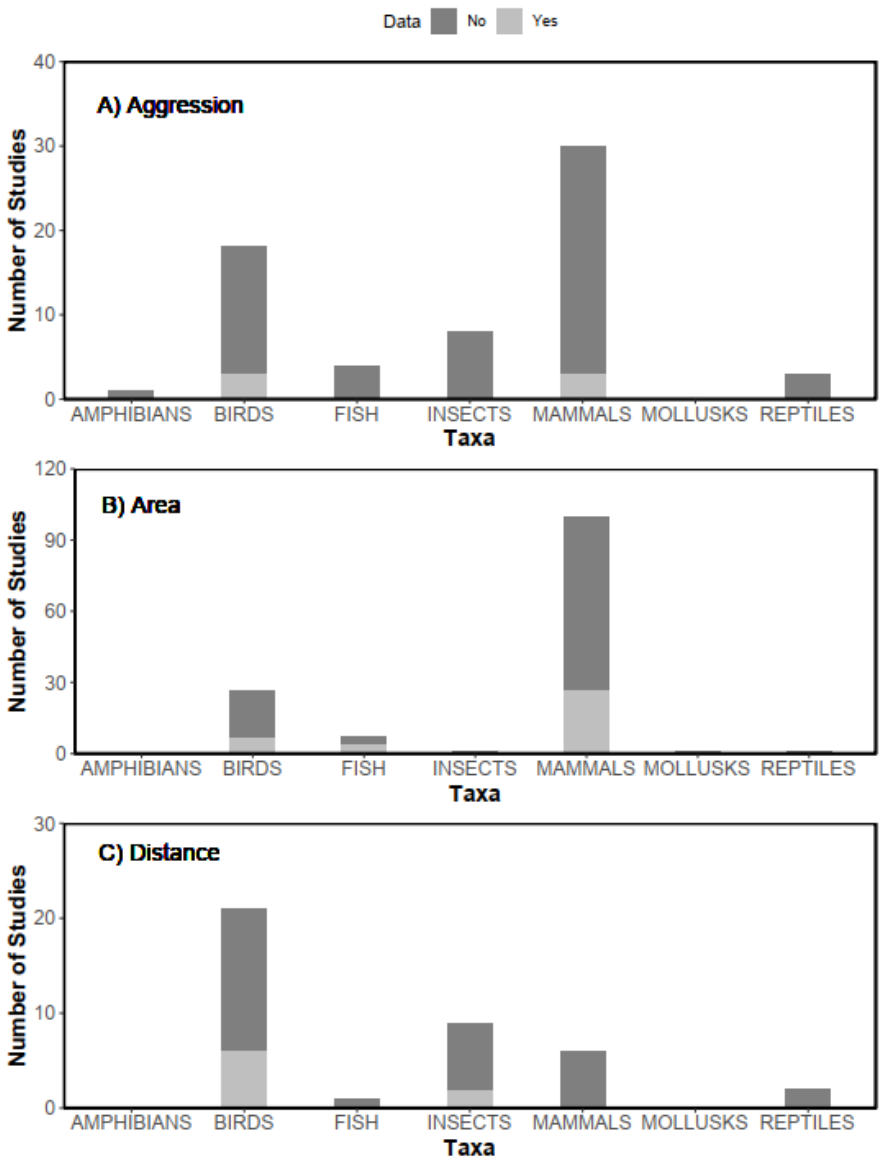

Figure 2.2 Papers which connected one of the given traits with food availability, compared by taxa and by whether each did (light grey) or did not have usable data (dark grey).

2.4.2 Consistency of optimal foraging responses

As predicted, foragers did not show a consistently negative or positive relationship between changes in food availability and changes in aggression (Aggression Response = 0.03, SE = 0.18, Standardized Effect Size (SES) = 0.07, Fig. 2.4). In three studies foragers increased their aggressive behaviour in response to increasing food availability, and in three studies they

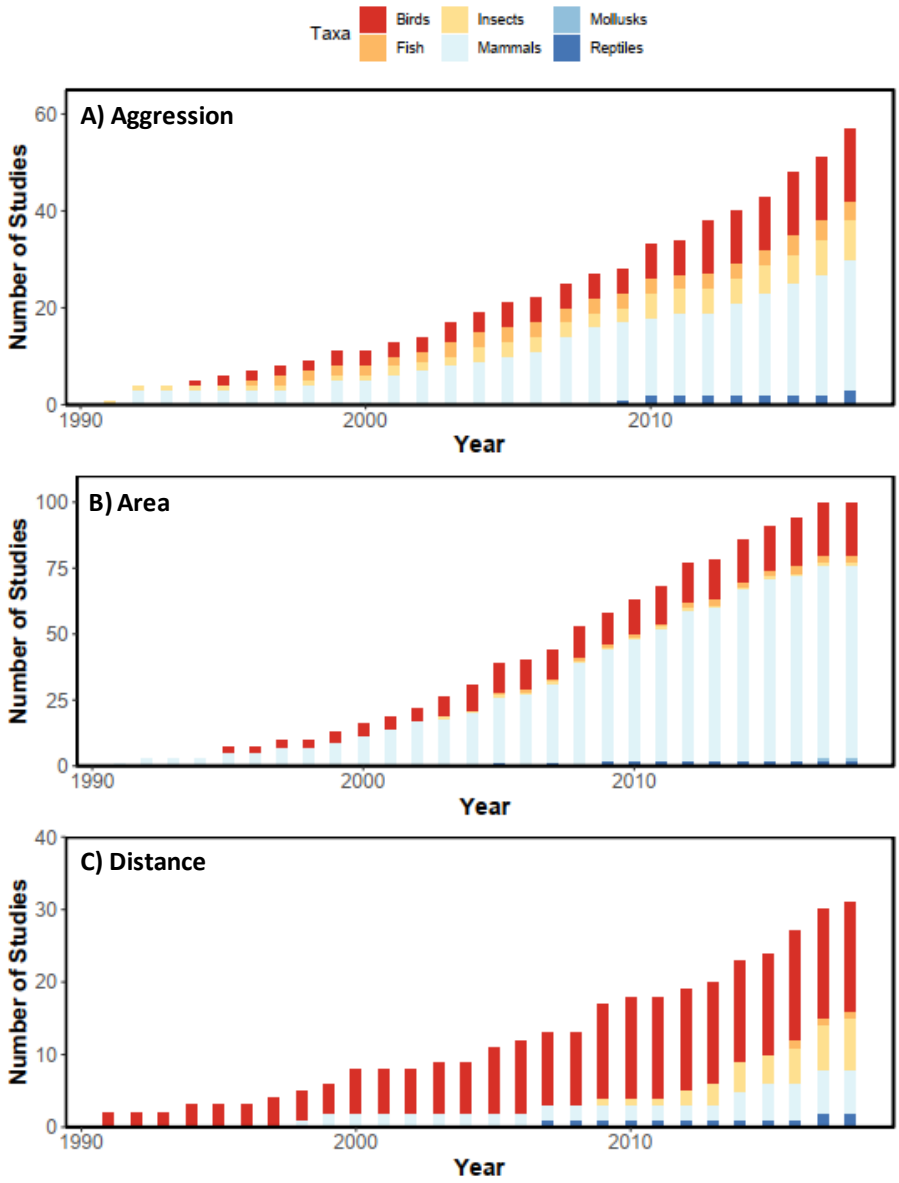

Figure 2.3 Cumulative number of papers which connected one of the given traits with food availability over time, broken down by taxonomy.

decreased their aggression. For home range, foragers were more likely to show a negative relationship with food availability than a positive one, but this was not a strong effect (Home Range Response = -0.27, SE = 0.07 SES = -0.63). In 25 studies foragers shrank their home ranges in response to increasing food availability, and in 10 studies they expanded them. Lastly, foragers

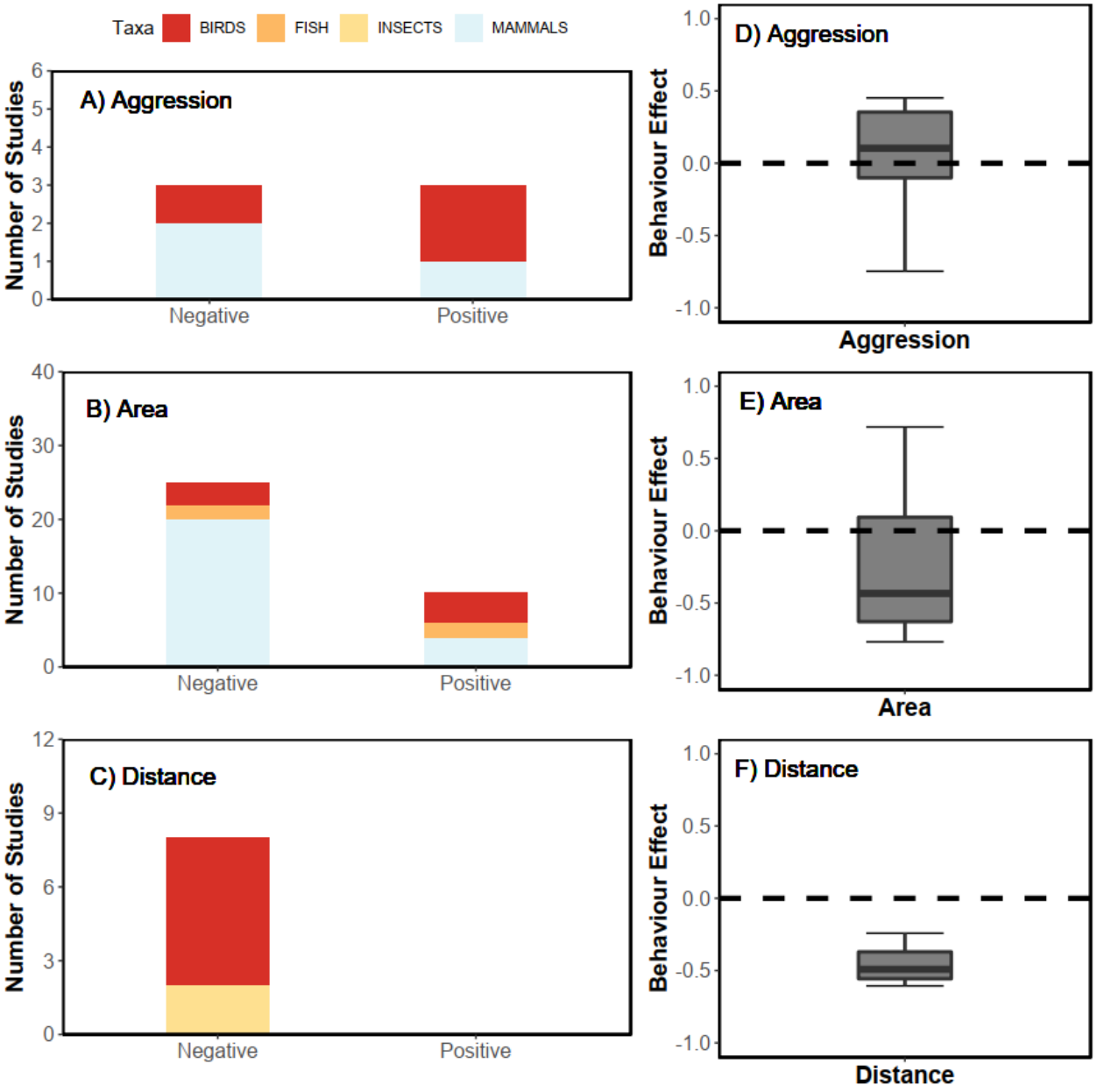

Figure 2.4 Consistency of behavioural effects within extracted papers. (A-C) Studies of the three given traits (broken down by taxa) and whether they showed a positive or negative relationship with food availability. (D-F) Box plot of effect sizes (r) for each of the given traits.

consistently showed a negative relationship between changes food availability and changes in feeding distance (Feeding Distance Response = -0.46, SE = 0.05, SES = -3.50). In all eight studies

with extractable data, foragers decreased their feeding distances in response to increased food availability.

Consistent with the vote-counting approach, studies in the meta-analysis assessing feeding distances were more likely to show a negative response with food availability than studies of home range size, but not significantly so, due to high variability among studies (SES = -0.34, p = 0.18, Fig. 2.5). Study trait (distance vs. area) was one of the most consistently informative predictors, included in six of the 13 best performing models. Additionally, larger increases in food availability were associated with larger negative responses in the two behaviours, although not significantly so (Mean = -1.11 $\frac{trait\ r}{food\ r}$, 95% CI = -2.59 – 0.37, p = 0.14). The size of the change in food availability was also a consistently informative predictor, included in six of the 13 models.

2.4.3 Evaluating potential constraints

1) **Predator Type**: Mammals were significantly more likely to show a negative response than endotherms / invertebrates (Fig. 2.5, SES = -0.60, p = 0.02). Birds were not significantly more likely to show this response (SES = -0.09, p = 0.73). However, predator taxonomy was only infrequently informative and was only included in two of the 13 models.

2) **Prey Mobility**: Mobility was the least informative predictor in this analysis and was not included in any of the best performing models.

3) **Prey Seasonality**: A seasonally fluctuating food source appeared to decrease the likelihood of a negative response to food availability, though this was not a significant effect (SES = 0.36, p = 0.16). Seasonality was one of the most consistently informative traits and was included in six of the 13 models.

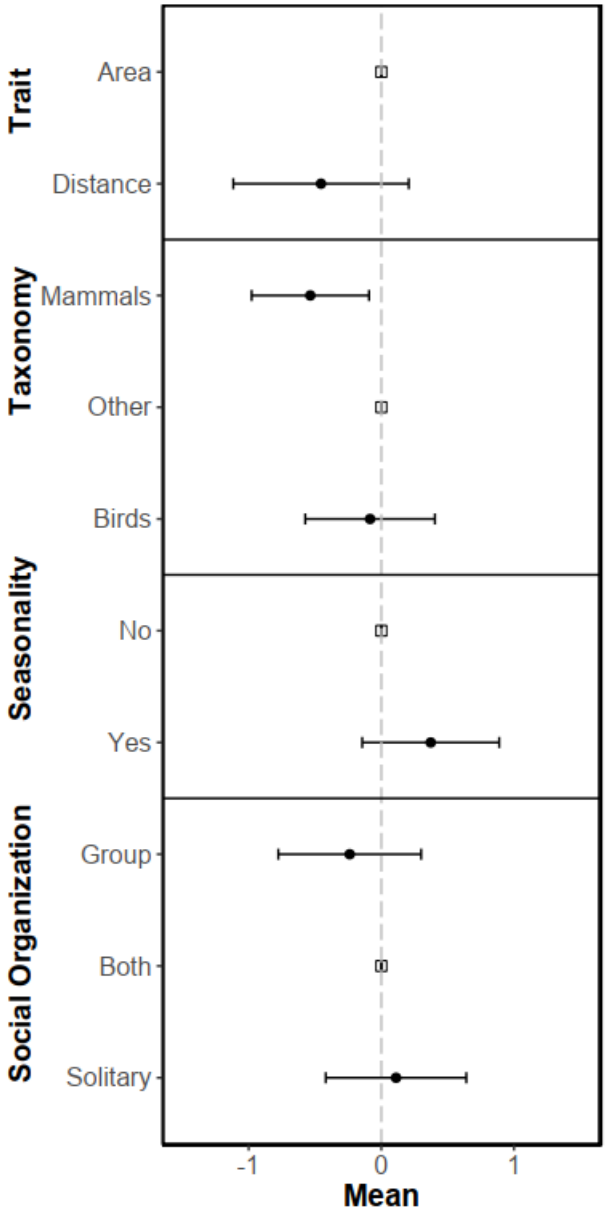

Figure 2.5 Model averaged parameter effect sizes from meta-analysis. For each factor, one level is set at 0 as a reference for comparison (white boxes), whiskers are 95% confidence intervals around the mean. Meta-analysis only included studies on home range or feeding distance.

4) **Predator Social Organization**: Social organization did not have a large effect on the response seen. While solitary foragers were slightly less likely to show a negative effect than those with mixed social organization (SES = 0.10, p = 0.68), and group foragers were slightly more likely to

show a negative effect, both of these effects were non-significant (SES = -0.22, p = 0.39). Social organization was also only infrequently informative and was only included in two of the 13 models.

5) **Predator Body Mass**: Body mass also did not have a large effect on the response seen. Foragers with higher body mass were slightly more likely to show a negative response with food availability, although not significantly so (Mean = -0.48 $\frac{trait\ r}{tonne}$, 95% CI = -2.13 – 1.17, p = 0.57). Body mass was infrequently informative and was only included in one of the models.

2.5 Discussion

Predicting the behavioural responses of foraging animals to disturbance events can prove difficult. Optimal foraging responses form an important theoretical basis for understanding behavioural change, but a host of different constraints and factors can result in varying context-specific behavioural outcomes. However, there may be some populations for which the predicted optimal foraging responses are most likely to be followed. Specifically, regarding predictions of increased forager space-use with decreased food availability, these may be most likely to be followed for mammals, and for foragers with seasonally stable food sources. While prey mobility has been seen to act as an important constraint on dietary responses to changing food availability (Sih and Christensen 2001), it does not appear to have such an effect on the space-use decisions of foraging animals. In response to reduced food availability, mammals were significantly more likely to expand their home range or lengthen their feeding distances than ectotherms / invertebrates (though this was not broadly included across potential models). In contrast, foragers targeting seasonally variable prey were less likely to expand their home range or lengthen their feeding distances (though this was a nonsignificant effect, despite consistently being broadly included). While a variety of other factors showed small, occasionally informative effects (social organization

and body mass), we do not expect these to significantly inform predictions of animals' responses to disturbance.

Prey mobility is believed to affect the degree to which foragers follow the optimal diet model because the model predicts optimal active predator choice (i.e., attack probability, Sih and Christensen 2001). Prey mobility can affect encounter rates and catchability, resulting in differences between active choice and the realized diet (Werner and Arnholt 1993). Because of this, responses should more clearly match optimal diet predictions if dietary studies measured attack probabilities, rather than diets themselves, but this is rarely the case. We predicted that similar issues of predictability might cause prey mobility to affect space-use responses as well. Changing space-use can be costly, so foraging animals should only do so if it would increase the energy benefit of the territory (Adams 2001). However, it can be difficult for animals to tell in advance what the benefit of a territory will be (Bollman et al. 1997), especially for foragers who cannot assess their food availability directly (Riechert 1981). Tracking patch quality can be more difficult when prey items are less predictable in space, and foragers that make less frequent contact with prey items are less frequently updating their perceptions of quality (Green 1984, Stephens 1987). This could make it harder or more time-consuming for foragers targeting mobile prey to assess the benefit of territory expansion than those targeting more spatially predictable sessile prey. However, prey mobility was the least informative factor in our analysis and does not appear to have affected the likelihood of territory expansion here.

Instead the most important factors affecting spacing responses appear to be prey seasonality and predator taxonomy. The spacing responses of foragers with seasonally varying prey may be less predictable. In some part, this may be due to alternate energy strategies employed by foragers facing seasonal declines in energy availability (i.e., hibernation / torpor, Geiser 1998, Humphries

et al. 2003). On the other hand, the spacing responses of mammals may be more predictable. This could be in part due to the developed nervous system of vertebrates, or the energetic demands of an endothermic lifestyle (Sih and Christensen 2001). It is also notable that the spread of studies among taxa reinforces this difference. While studies on home range had weaker behavioural effects than those of feeding distance, a greater proportion of studies on home range were based on mammals.

Body size did not have a large effect on the strength of spacing responses and there are a couple potential explanations for this. First, while body size correlates with brain size, a broader suite of papers point to metrics of relative brain size (e.g., encephalization quotient, residual methods, among others, Deaner et al. 2000, Sol et al. 2005), or the size of specific brain structures (Healy and Rowe 2006), as better reflections of cognitive ability, making comparisons based on overall body size less useful. Additionally, while larger bodied animals typically have higher energy demands, they also tend to have higher energy intake rates, corresponding with allometric consumptive traits (ex. gape width (Dunic and Baum 2017, Mihalitsis and Bellwood 2017) and digestive capacity (Demment and Van Soest 1985, Van Soest 1996).

One clear pattern is that the foraging response literature is dominated by studies on mammals and birds. This makes sense as conservation, behaviour, and biodiversity research as a whole are biased towards vertebrate species, particularly mammals and birds (Bonnet et al. 2002, Clark and May 2002, Rosenthal et al. 2017, Titley et al. 2017). These biases in attention apply not only to research, but conservation efforts as well (Seddon et al. 2005, Mammides 2019). Even among mammals there is a bias in conservation research towards species with higher body mass (dos Santos et al. 2020), consistent with the paradigm that conservation effort is preferentially inspired by and directed toward charismatic megafauna (Leader-Williams 2000, Ducarme et al. 2013, Thompson

and Rog 2019). However, these biases in study taxon raise important concerns about theoretical predictions, namely the extent to which they are generalizable when they have been primarily supported by field studies on specific taxa. Given that mammals were seen to be more likely to follow optimal foraging theory predictions here, this is a heightened concern.

Differences in study spread between mammals and birds among the three traits likely draw from the different methods used to measure space-use and their relative ease of use with different taxa. For example, radio and satellite telemetry devices are an exceedingly common method to determine animal home ranges. However, they can be cumbersome and may not be easily carried by smaller animals, or may increase movement costs, particularly among flying and swimming animals (Cooke et al. 2004, Barron et al. 2010). To reduce transmitter drag among birds, Hill and Robertson suggest a transmitter mass no more than 5% of the mass of the animal (Hill and Robertson 1987). While recent advances in technology have allowed for exceedingly small tags (Bridge et al. 2011), tag size has limited telemetry studies on some of the smallest birds. As a result of these issues, radio and satellite telemetry are overrepresented in studies of large mammals compared to birds or smaller mammals.

We sought to directly calculate effect sizes for changes in food availability and three important foraging traits. Doing so allowed the inclusion of studies which reported both food availability and one of the traits but did not explicitly test the effects of one on the other. However, it is now clear that while there are several articles containing some information on both food availability and foraging behaviour, many did not report this data in a manner sufficient to be included in this quantitative analysis. Additionally, attempts to maintain consistency between the three traits (by developing a shared set of food availability search terms) resulted in vastly different numbers of search results between them. This highlighted a wealth of studies which could potentially inform

these relationships but could not be explored due to time constraints. As a result, further study of these relationships might better focus search on a single behaviour, to ensure results aren't overly broad, and to employ a mixed approach, exploring the effect of potential constraints on continuous data where it is available and binary data where it is not.

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2.7 Contribution of Authors

RFS and SAK developed the primary research questions and all authors contributed to the study design. RFS performed all searches, extracted the relevant data, performed analyses, and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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3. Behavioural shifts drive reorganization of reef fish networks after coral mortality

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Robert F. Semmler[1], Nathan J. Sanders[2], Paul J. CaraDonna[3], Andrew H. Baird[4], Xin Jing[2,5], James P.W. Robinson[1], Nicholas A.J. Graham[1], Sally A. Keith[1]

[1]Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, UK

[2]Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, 05405, USA

[3]Chicago Botanic Garden, Glencoe IL, 60022, USA

[4]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, 4811, Australia

[5]Gund Institute for Environment, University of Vermont, Burlington VT, 05405, USA

3.1 Abstract

The direct and indirect effects of climate change can affect, and are mediated by, changes in animal behaviour. However, we lack sufficient empirical data to assess how large-scale disturbances affect the behaviour of individuals, which in turn scales up to influence communities. Here we investigate this response pathway by focusing on the foraging behaviour of coral-feeding fishes before and after a mass coral bleaching event. In response to substantial coral mortality, coral-feeding fish consumed increasingly broad diets, weakening their prey preferences. This simultaneous dietary expansion of multiple species occurred in such a way that all species reduced their consumption of bleaching-sensitive *Acropora*, instead consuming a variety of other coral genera. This resulted in decreased resource overlap, as well as substantial rewiring of the consumer-resource interaction network. Our work shows that behavioural responses to disturbance can have significant effects on community structure. The work illustrates an existing response pathway, whereby a reduction in food availability affects the structure of interaction networks through changes in dietary specificity and overlap. This pathway may prove informative to disturbances within other similarly structured communities, such as plant-pollinator networks. The adaptive community response seen here also raises significant questions about the continued fate of species within this community, considering coral mortality has substantially reduced populations of coral-feeders elsewhere.

Keywords: *behavioural plasticity, consumer-resource interactions, climate change, interaction rewiring, coral bleaching, resource partitioning*

3.2 Introduction

Disturbances, including those that result from climate change, can alter the behaviour of individuals and reshape the dynamics of populations and communities (Sih et al. 2011, Van Buskirk 2012). An increasingly prevalent severe climatic disturbance is thermal bleaching and subsequent mortality of tropical coral reefs (Glynn 1993). Coral bleaching events are now five times as frequent as they were in the early 1980s (Hughes et al. 2018) and cause extensive mortality within a very diverse, yet sensitive ecosystem over a very large spatial scale (Hughes et al. 2017). Coral bleaching affects behaviour of reef-associated fishes (Keith et al. 2018). For example, the alteration of visual or olfactory cues following bleaching affects behaviour of juvenile fish at settlement and when seeking shelter from predators (Coppock et al. 2015, Boström-Einarsson et al. 2018). In many cases, it is unclear whether these behavioural shifts are adaptive (Tuomainen and Candolin 2011). However, while it is clear that bleaching affects fish behaviour, it is unclear how this behavioural change might propagate through coral reef communities to impact the structure of ecological networks.

Disturbance can affect behaviour by altering food availability (bottom up effects, Wilson et al. 2020), prompting changes in food use by foragers. In coral reefs, bleaching events often result in substantial coral mortality, which in turn reduces the food availability for coral-feeding fish such as butterflyfishes (Family: *Chaetodontidae*) (Keith et al. 2018). Butterflyfishes are a diverse group of closely related species that exhibit considerable variation in dietary specialization (Cole and Pratchett 2014). For a number of butterflyfish species (particularly *Chaetodon spp.*), their survival critically depends on the abundance of coral prey, and their populations have declined as a result of bleaching-induced coral mortality (Wilson et al. 2013). Additionally, for many butterflyfishes, reductions in coral cover cause a decline in body condition (Pratchett et al. 2004). In other fish

species, reduced body condition has caused negative effects on growth and reproductive output (Jones 1986, Kerrigan 1997), though this has not been directly tested for butterflyfishes (see Berumen and Pratchett 2008).

Optimal foraging theory posits that unnecessary expenditures of energy should be selected against, as should behaviours that place unnecessary restrictions on energy intake (MacArthur and Pianka 1966). As such, when food availability is low, the optimal diet model predicts that foragers will expand their diets in response (Emlen 1966). While the ability of foragers to expand their diets may be limited by disturbances that reduce the diversity of available food items (e.g., Haley et al. 2011, Folks et al. 2014), predictions of dietary expansion have been confirmed in a variety of systems (e.g., Owen-Smith 1994, Rödel et al. 2004). Additionally, a review of 134 studies which tested the assumptions of optimal diet theory found that the factor most likely to coincide with a system failing to follow the optimal diet model was prey mobility (Sih and Christensen 2001). Therefore, in response to mortality of their immobile coral prey, coral-feeding butterflyfishes should expand their diet breadth, weakening their dietary preferences.

Many butterflyfishes have altered their diets after coral mortality, decreasing the proportion of bites taken from bleaching-sensitive *Acropora corals* (Pratchett et al. 2004, Keith et al. 2018, Zambre and Arthur 2018). However, increases in dietary breath may not necessarily stem from weakening dietary preferences, but could instead be a direct response to changes in prey abundance and composition (i.e., prey switching) (Murdoch 1969, Cornell 1976). Rather than involving a weakening of prey preferences, this pattern of prey switching, appearing typically in populations of generalists, shows species shifting their preferences towards the most abundant species. Distinguishing between these two scenarios will require us to quantify how the strength of dietary preferences responds under reduced food availability.

One important consideration of dietary shifts is their potential to affect resource overlap. Because many of these species focus a large portion of their attention on *Acropora*, dietary expansion by them could lead to reduced resource overlap. If resource overlap among butterflyfishes decreases, this would signal an adaptive community response, with species spreading their efforts toward different groups in light of *Acropora* mortality. On the other hand, resource overlap could increase instead, particularly if species shift their focus onto a specific, second-most preferred genus. Increased resource overlap could increase the likelihood of competitive exclusion within the system, as greater partitioning tends to allow for more stable coexistence (Chesson 2000). From prior studies it is clear that coral bleaching events cause species turnover which is spread unequally across assemblages, leading to biotic and functional homogenization of fish communities (Richardson et al. 2018). By quantifying the link between dietary shifts and resource overlap, we can further explore potential pathways for species turnover, and better understand the effects of coral bleaching and subsequent mortality on butterflyfish communities.

The effect of dietary change on consumer-resource interactions offers a unifying thread between individual behaviour and ecosystem structure. Consumer-resource interactions are the individual links that together create community structure (Elton 1927, Hutchinson 1959). When dietary preferences weaken, species are expected to develop new interactions with previously unconsidered food items. As a result, the consumer-resource interaction network can experience "topological rewiring", with new connections being made in place of those that were lost (Burkle and Alarcon 2011, Poisot et al. 2012). "Interaction strength rewiring", in contrast, occurs when species shift their relative use of different habitats or resources (Bartley et al. 2019). Significant cases of topological rewiring have been observed following non-native species invasion (Montero-Castaño and Vilà 2016), variable phenology in plant-pollinator networks (CaraDonna et al. 2017),

and experimental species removals in seed dispersal networks (Costa et al. 2018). In a sense, dietary changes among foragers should cause networks to rewire, whether topologically (foragers change food items in their diet) or through interaction strength (foragers alter the frequency of food items in their diet). If dietary preferences weaken following bleaching as predicted, butterflyfish-coral networks should experience topological rewiring.

Similarly, if dietary preferences weaken as predicted, then interaction networks should also become more even, particularly due to their unique pre-bleaching structure. Coral assemblages are typically dominated numerically by bleaching-sensitive *Acropora* species (Renema et al. 2016), which provide the majority of coral tissue consumed by butterflyfishes (Keith et al. 2018). As they are more susceptible to bleaching, these *Acropora* corals often face the greatest degree of mortality (Marshall and Baird 2000, Loya et al. 2001). Because of this, the post-mortality coral assemblage is expected to be substantially more even. This combination of increasingly even coral assemblages, with broader fish diets would cause consumer interactions to become dispersed more evenly among potential linkages as well. These two concepts, rewiring and increasing interaction evenness, are closely related. In fact, increasing dietary evenness is itself a type of rewiring (interaction strength rewiring, defined above). Exploring the connection between behavioural change and consumer-resource interactions should yield important insights, but time series data on consumer-resource interactions, particularly following severe disturbance, is scarce.

Here, we determine how dietary preferences, niche partitioning, and consumer-resource interactions are affected by a coral-bleaching event with extensive coral mortality. We use a dataset spanning three years, 14 butterflyfish (consumer) species, 131 coral (resource) species, and three locations. We quantify the extent to which foraging behaviour of coral-feeding fishes has changed in response to a large decrease in food availability following coral bleaching. Specifically, we test

the hypothesis that (i) when food availability decreases, fish weaken their dietary preferences, and that (ii) weakened preferences leads to less dietary overlap (i.e., increased niche partitioning) among competing species. Finally, we (iii) test whether behaviourally-mediated diet shifts restructure interactions via rewiring and explore the implications for corallivorous fish communities. Specifically, we focus on topological rewiring of interaction networks.

3.3 Methods

3.3.1 Study system

Our study was conducted on the reef flats and crests (1 – 3 m depth) at three sites on the north/northwest coastline of Iriomote, Japan; Nata (24.43 N, 123.79 E), Sonai (24.38 N, 123.75 E), and Unarizaki (24.43 N, 123.76 E) (Fig. S3.1). Data were collected for three years: 27 May to 11 June 2016, 13 July to 17 July 2017, and 12 July to 18 July 2018. In May and June 2016, there was a mild, but notable thermal anomaly around Iriomote, elevating sea surface temperatures 1.0–1.5 °C above the 30 year mean. Combined with unusually calm conditions, this resulted in widespread coral bleaching, with the first signs noticeable to observers on the final day (June 11) of sampling in 2016. At the time of completion of the 2016 surveys there had been no coral mortality; however, one year later, we observed coral mortality of ~65% (Baird et al. 2018, Keith et al. 2018). These temperature differences alone are unlikely to have a substantial effect on behaviour; behavioural changes in laboratory experiments of adult reef fish have only been documented at temperature increases to of 3°C or higher above ambient conditions (e.g., Allan et al. 2015). We compared coral cover and butterflyfish diets before and after this mass mortality event, investigating changes in coral cover as a predictor of dietary change. As our focus is specifically on the effect of coral mortality, rather than bleaching itself, we are confident in

Species	Obligate vs Facultative	% *Acropora* in Diet Before Mortality	% *Acropora* in Diet After Mortality	Included in Tests of…		
				Dietary Change	Resource Overlap	Network Rewiring
Chaetodon argentatus	Facultative	52% 71 of 136 bites	0% 0 of 70 bites			✓
Chaetodon baronessa	Obligate	50% 67 of 133 bites	4% 8 of 171 bites			✓
Chaetodon bennetti	Obligate	9% 6 of 65 bites	No Data			✓
Chaetodon citrinellus	Facultative	52% 699 of 1335 bites	14% 143 of 1034 bites	✓	✓	✓
Chaetodon kleinii	Facultative	13% 11 of 84 bites	No Data			✓
Chaetodon lunulatus	Obligate	51% 1033 of 2010 bites	19% 490 of 2569 bites	✓	✓	✓
Chaetodon melannotus	Obligate	0% 0 of 7 bites	0% 0 of 9 bites			✓
Chaetodon ornatissimus	Obligate	53% 36 of 68 bites	35% 28 of 81 bites			✓
Chaetodon plebeius	Obligate	12% 34 of 282 bites	3% 8 of 307 bites	✓	✓	✓
Chaetodon rafflesii	Facultative	4% 4 of 97 bites	1% 4 of 279 bites		✓	✓
Chaetodon reticulatus	Obligate	71% 49 of 69 bites	No Data			✓
Chaetodon speculum	Facultative	3% 2 of 77 bites	0% 0 of 31 bites			✓
Chaetodon trifascialis	Obligate	94% 2273 of 2430 bites	64% 1185 of 1857 bites	✓	✓	✓
Chaetodon unimaculatus	Obligate	0% 0 of 21 bites	0% 0 of 29 bites			✓

Table 3.1 List of all species included in the study. Use of species in certain portions of the analysis was limited by the amount of replicate observations. Four species, colored in dark gray, were numerically abundant over multiple locations and time-periods, allowing their inclusion in all steps of the analysis. Coral-feeding designations taken from Cole and Pratchett 2014. Percentages of *Acropora* in diets calculated based on the number of bites, summed across all individuals of a species.

establishing the 2016 surveys as "pre-mortality". Table 3.1 lists all 14 *Chaetodon* species included in this study and in which sections of the analysis they were included.

3.3.2 Sampling of butterflyfish and coral assemblages

We estimated butterflyfish abundances using 50 m belt transects (English et al. 1997). We counted and recorded the species identity of every butterflyfish within 2.5 m on either side of the transect tape. We ran six separate transects at each site per year. As transect positioning was constrained by the size and shape of the site, they were very consistent across the years. Transects were placed at approximately 1 m depth parallel to the reef crest, this placement focused attention on the areas of the reef most heavily used by coral-feeding butterflyfishes and in the same area of the reef where our feeding observations were conducted. We estimated coral cover using 50 m point intercept transects (Rogers et al. 1983). We recorded the benthic substrate every 0.5 m along the transect, including the species identity of hard (scleractinian) corals. Transect placement was consistent with butterflyfish assemblage sampling, and butterflyfish counts were completed first, prior to coral sampling, to limit any effects of diver presence.

3.3.3 Butterflyfish-coral interaction sampling

To measure butterflyfish diets, we followed a focal fish on either snorkel or SCUBA for three minutes and recorded every bite they took on the substrate, along with the species identity of scleractinian corals that were bitten (*following* Pratchett 2005). Butterflyfish are appropriate for on-site behavioural analysis as they are typically undisturbed by diver presence (Kulbicki 1998). During the observation, the observer maintained a distance greater than the fish's perceived flight initiation distance (FID, Ydenberg and Dill 1986), generally 2-4 m and the observer minimized their movement. Many butterflyfish species are pair-forming so to avoid dependence in our observations, only one of the two fish in each pair was observed. To avoid repeat sampling of the same fish, the observer travelled along the reef in a U-shape search pattern (Chidlow et al. 2005), which prevents observers from moving back through areas already sampled. The width of the U-

shape was approximately twice the width of the average foraging territory (varied between species) (e.g., 60-170 m^2 (18-30 m width) for *C. lunulatus*, Berumen and Pratchett 2006). All feeding observations were performed by AHB, and the following contextual variables were recorded for each observation: date, time, and weather. All sampling occurred between 08:00 and 16:00, with daily observation times limited by tide height (> 1 m). In over 800 hours in the field, we did not observe a single predation event on butterflyfishes, consistent with the known scarcity of these occurrences (Ehrlich 1975). As such we do not expect predation to pose a major factor in butterflyfish behaviour during these observations.

3.3.4 Data analysis

There are two primary elements to the dietary breadth of a species: (i) the strength of its dietary preferences, and (ii) the actual, realized diet, which may be more or less evenly distributed as a result of these preferences. To investigate whether both dietary elements changed in response to reductions in prey, we used two related analyses. First, to evaluate change in the strength of dietary preferences, we quantified the consistency in dietary preferences of individuals within each given species. Second, to evaluate whether there has been a significant change in the evenness of realized diets, we test whether they fit a null expectation of change based on shifts in the evenness of coral assemblages. These methods are explained below.

3.3.5 Quantifying changes to interspecific consistency in preferences

A species was categorized as having strong dietary preferences if all individuals of the species consistently preferred the same coral genera. We used dietary data from the individual observations to calculate the selectivity of each individual fish for each of the seven most abundant coral genera in the dataset (*Acropora*, *Favites*, *Galaxea*, *Goniastrea*, *Montipora*, *Pocillopora* and *Porites*) using Ivlev's Electivity Index (Ivlev 1961). This metric compares the amount of bites on

each food type against its abundance within the habitat. It indicates how much a forager preferentially seeks out particular food items and scales from complete avoidance (-1) to exclusive selection (1) (Ivlev 1961). These seven coral genera account fo > 90% of all bites on hard coral. All other genera were consumed too infrequently to generate reliable selectivity values. This analysis included the four most commonly observed fish species, (*Chaetodon citrinellus, C. lunulatus, C. plebeius,* and *C. trifascialis*), which comprised ~ 80% of all foraging observations. All other species were excluded from the analysis due to limited observations.

Dietary selectivity values for each individual fish on each of the coral genera were then compared pairwise to all other fish of the same species at that same year and location. Selectivity values were compared using Spearman rank-order correlations so that consistency in ranking could be evaluated. Resulting Spearman correlation coefficients were rescaled to ensure that all values were positive, and that they matched the beta distribution, which is well suited to response variables bounded in both directions (Ospina and Ferrari 2010). The rescaling performed was: ($y_1 = (y_0 + 1) / 2$), such that our coefficients scaled from 0 to 1. The coefficient for two individuals with the opposite order of food preferences is zero; while the coefficient for two individuals with the same order of preferences is 1 (Fig. 3.1). In this way, a mean coefficient close to 1 indicates strong adherence to a consistent ranking of dietary preferences, and a mean coefficient close to 0.5 indicates no consistent ranking. These values are hereafter referred to as "preference coefficients" and reflect the strength of dietary preferences. It should be noted that these values only reflect dietary selection on hard corals, to focus on changes in hard coral consumption after the coral mortality event, and therefore do not include consumption of other prey, such as non-coral invertebrates.

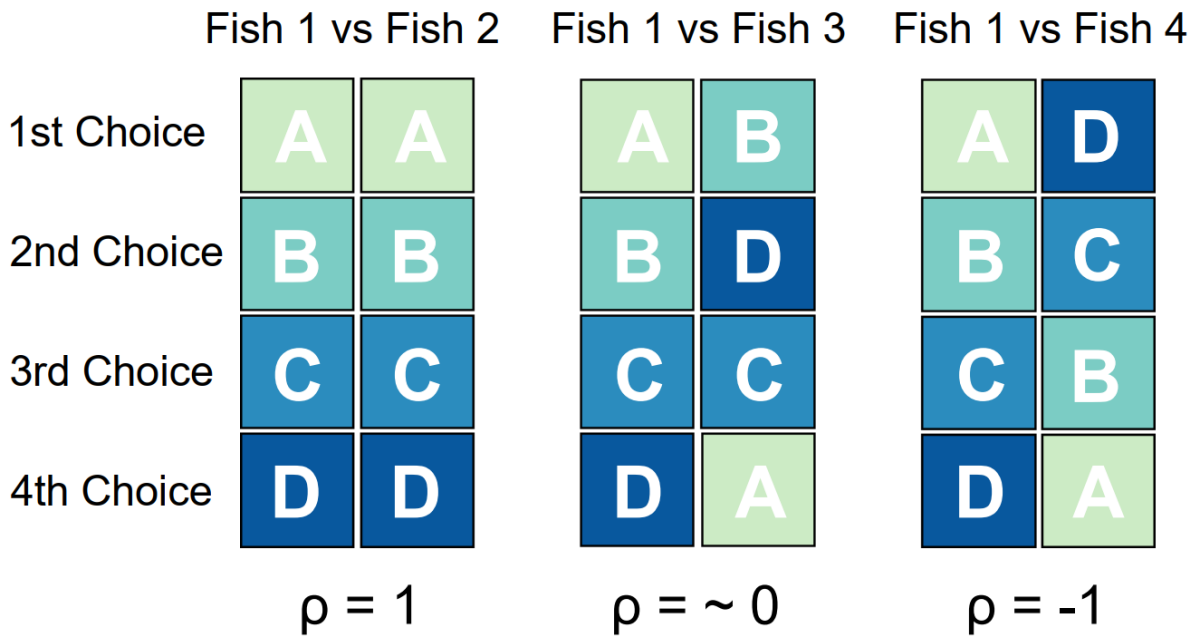

Figure 3.1 Schematic of dietary preference comparisons. Food items (coral genera, lettered A-D) were ranked from most to least preferred based on Ivlev's Electivity Index. Preference rankings of a given fish were compared against all others of the same species in the same time and location. They were compared with Spearman's rank correlation, rescaled where $\rho = 1$ reflects the exact same order of preferences, and $\rho = -1$ reflects the exact opposite order of preferences.

We used a generalized additive mixed model with a beta distribution (Beta GAMM) to model the strength of dietary preferences as a function of coral cover. Specifically, we used a one-inflated beta distribution for the model. This model structure is well suited to fit data when the response value is bounded, $0 < Y \leq 1$ (Ospina and Ferrari 2010). Our model assesses the strength of dietary preferences as a function of hard coral cover at the site-level, with a fixed covariate for forager species. As each observation is a pairwise comparison between two fish, there was dependency among observations that shared the same fish individual. To account for this dependency, we used the identity of each of the two fish in the comparison as two separate random intercept effects. The optimal model was determined by backward model selection using Aikaike's Information Criterion (AIC), sequentially dropping terms from an initial full-model (following Zuur et al.

2007), which also included fixed covariates, Site, Year, and Pielou's evenness of the coral genera subset (Pielou 1966, calculated in package 'vegan', Oksanen 2019). All models were run in R 3.6.1 (R Core Team, 2019) using the package 'gamlss' (Rigby and Stasinopoulos 2005). Details on model selection are listed in Table S3.1. We predicted the strength of preferences for each species within the range of coral cover values for which is was observed. We generated 95% confidence intervals around these predictions using jackknife resampling, whereby we randomly subset the dataset to 80% of the observations, re-fitted the model and generated predictions on this subset, and repeated the process for 100 replicates (McIntosh 2016). These 100 jackknife predictions were ordered, and confidence intervals taken as the 5^{th} and 95^{th} values. Predictions were made specifically on one level of the random intercept effect. To test if relationships varied among species depending on their initial strength of preferences, we also fit an alternate model, which was structured the same way, but also included an interaction between hard coral cover and butterflyfish species, and compared via AIC.

3.3.6 Evenness of fish diets given altered coral assemblages

If the evenness of fish diets increased but was matched with an equivalent increase in the evenness of coral assemblages, then resource abundance, rather than weakening dietary preference, is likely to be driving observed diet shifts (i.e., prey switching). However, a large increase in the evenness of fish diets, with little change in the evenness of coral assemblages can be attributed to a weakening of preferences. We evaluate whether diets increased substantially in evenness, exceeding an expected level of change based on changes to coral assemblages.

We compare the evenness of coral assemblages and fish diets over time (i.e., in years before and after disturbance), with Hurlbert's Probability of Interspecific Encounter (PIE) (Hurlbert 1971). When randomly selecting an individual from a community, PIE represents the probability of

selecting the same species twice in a row, and thereby is an intuitive measure of community evenness. PIE was calculated at the species level for both the coral assemblage and for fish diets. For the coral assemblage, PIE was calculated for each transect individually, to use each transect as an independent replicate of coral assemblage structure. For fish diets, individual observations of a particular fish species from each of the three sites were summed together, as each individual observation contained too few prey species to calculate reliable PIE values. From these summed diets, we calculated an overall dietary evenness value for each species at each site and year. This analysis included the four most commonly observed fish species (as above).

3.3.7 Influence of disturbance on niche partitioning among coral-feeding fishes

To test the effect of disturbance on resource partitioning we compared matrices of overall resource use before (2016) and after (2017 + 2018) coral mortality. For both this, and the following network tests, it was important to maintain matrices and networks comparable in dimension and interaction richness. For this reason, and because of decreased butterflyfish abundance following coral mortality, in both efforts, values for the two years after disturbance were combined into a single matrix/network, to represent the post-mortality state overall.

Resource use matrices were then compared against null models (following Gotelli and Ellison 2013). For each condition, we generated a set of 1,000 simulated matrices for comparison with the observed matrix, to determine the likelihood of an equivalent degree of resource partitioning being observed by chance. Simulated matrices were generated such that dietary breadth (number of resources) consumed by each fish species was maintained, but specific resources consumed were randomly reshuffled. Resource-use matrices were computed at the genus level for the food resource (i.e., corals) and included all forager species that were observed frequently both before and after disturbance. Matrices included the same seven coral genera as above.

Observed resource use was compared with the null expectation via the Pianka niche overlap index (Gotelli and Ellison 2013). For any two species, the Pianka niche overlap index represents the proportion of resources used by either species that are shared by the two; values range from 0 (no shared resources) to 1 (all resources shared; Pianka 1973). For these resource-use matrices, Pianka niche overlap is the average pairwise niche overlap between all fish species. We also compute the Standardized Effect Size (SES) for the difference between the observed level of partitioning and the null expectation (Gotelli and McCabe 2002). While the proportional comparisons involved in this method do not require equivalent sampling, the fewer observations there are for any species, the greater likelihood of error around the proportional allocations of bites. For this reason, we included only those *Chaetodon* species which were observed at least eight times (≥24 min of feeding) in both time periods. This included the same four fish species as above, with the addition of *C. rafflesi*.

3.3.8 Change in forager networks following disturbance

Overall change in the structure of interaction networks was compared via a Komogorov-Smirnov test (Conover 1971) of the interaction probability distribution. Interaction matrices for each condition (before [2016] and after [2017 + 2018] coral mortality) were each converted into one long vector for this comparison. Interaction networks used for each analysis included all 14 species of butterflyfish and all 131 coral species. Matrices for all network analyses were rescaled based on the observed abundances of each butterflyfish species in each condition.

To evaluate interaction changes after disturbance, we also computed five network metrics that describe important aspects of network structure: connectance, Alatalo interaction evenness, Shannon diversity, nestedness, and network-level interaction specialisation (H2’). Connectance refers to the proportion of possible links between consumer and resource species which are present

within the network. An increase in connectance is likely if butterflyfish are forming new connections with corals previously unconsidered (interaction rewiring). Diversity and evenness of the interaction network refer to the diversity and spread of individual interactions (i.e. bites) among these possible links (Alatalo 1981). These are also expected to increase as fish species with weaker preferences will have a greater spread of their interactions among corals. Nestedness is a complex measure of network structure, and generally defines a system where there is a core group of generalists, and a set of specialists which primarily interact with generalists (Nielsen and Bascompte 2007). Interaction evenness, Shannon diversity, and nestedness of the networks before and after disturbance were compared against those of null models to determine significance of changes. Null models were generated such that the observed number of interactions within the network is maintained (i.e., observed connectance), but interactions are randomized in proportion to their observed frequency between consumer I and resource j (following Vázquez et al. 2007). All network metrics were calculated using the 'bipartite' package in R (Dormann et al. 2009).

Lastly, we assessed temporal change in interaction networks (temporal β-diversity) and partitioned β into its inherent components using package 'Betalink', following Poisot et al. (2012). Changes in interaction network structure (β_{int}) can be separated into the contribution of this change due to species turnover (β_{st}- interactions gained or lost due to species gains or losses) and the contribution due to topological interaction rewiring (β_{rw}-interactions gained or lost among species present in both years). Betalink quantifies these three elements (β_{int}, β_{st}, β_{rw},) as well as the amount of species turnover (β_s) between networks. Specifically, we wished to understand the degree of change in network structure following bleaching induced mortality (2016 vs 2017), and whether networks continued to change two years after bleaching (2017 vs 2018). It's for this reason that the two years post-mortality are treated separately for this piece of the analysis. To evaluate interaction

rewiring in this system, we specifically wished to understand whether there was substantial chan first consider whether there was substantial change in network structure before and after coral mortality (2016 vs 2017 vs 2018) (i.e., large values of β_{int}), then whether a large portion of this change was due to rewiring (i.e., $\beta_{rw} > \beta_{st}$).

3.4 Results

We recorded the diets of 537 individual fish from 14 different species based on observations of 12,618 bites on hard coral tissue (11,406 on the select seven coral genera specified previously). We recorded a total of 107 unique hard coral species on benthic transects; 60 in 2016, 48 in 2017, and 55 in 2018. The number of coral species per transect was not significantly different among years (ANOVA: $f = 3.696$, $p = 0.060$).

There was a significant difference in total butterflyfish abundance among the three years sampled, with abundance decreasing in 2018 (Table S3.2, Kruskal-Wallis: $df = 2$, $X2 = 17.05$, $p < 0.001$). Total butterflyfish abundance was 175 in 2016 (avg = 11.7 per transect), 223 in 2017 (12.4 per transect) and 102 in 2018 (5.7 per transect). In some sense, having lower abundances in 2018 allowed for pre- and post-mortality networks that were more comparable in size than would be otherwise if abundance remained the same. The pre-mortality network had 14 fish species and 104 coral species (interaction richness = 238) and the post-mortality network contained 11 fish species and 108 coral species (interaction richness = 293). Changes in total abundance occurred without substantial change in the rank-order of fish species. Rank-orders were strongly correlated between 2016 and 2017 ($S = 89.06$, p-value < 0.001, $\rho = 0.80$), and between 2017 and 2018 ($S = 109.4$, p-value $= 0.002$, $\rho = 0.76$).

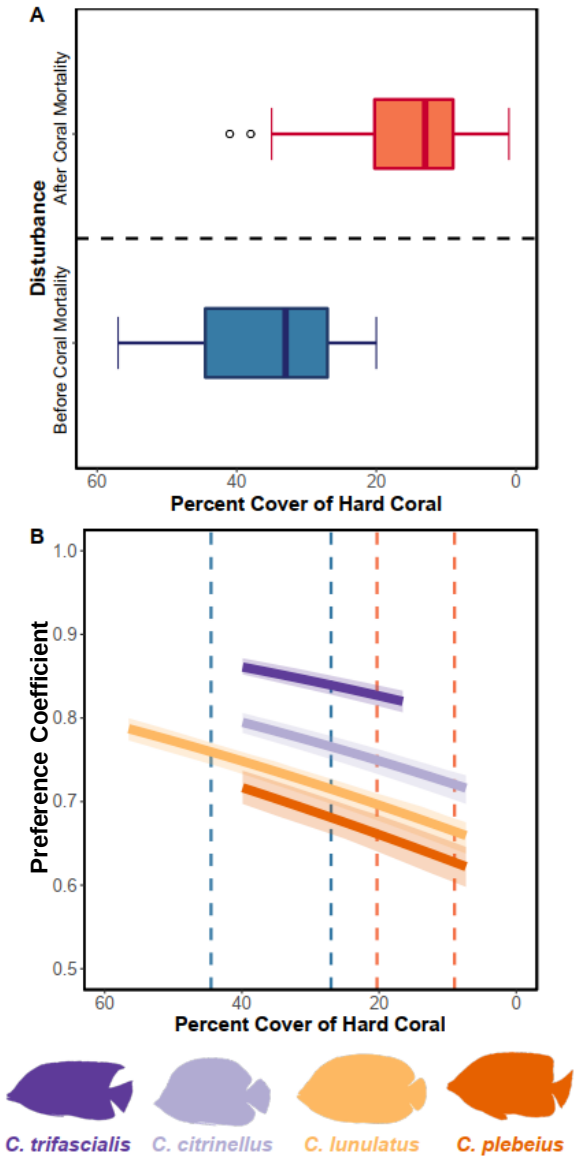

Figure 3.2 A) Loss of hard coral cover (%) due to coral bleaching. Transects were set on shallow (1m) reef crests. B) Reaction norm plot of dietary plasticity with disturbance, under the additive model. Solid lines are GAMM predictions of preference coefficient for each species across the range of observed coral cover, with 95% confidence intervals generated from jackknife resampling of 80% of the entire dataset. Dashed lines indicate the interquartile range of hard coral cover in the pre- (blue) or post-coral-mortality (orange) condition, matching panel A.

3.4.1 Quantifying changes in consistency in preferences

Coral cover decreased sharply after bleaching in 2016 (Fig. 3.2A). Notably, cover of bleaching-sensitive *Acropora* corals decreased from an average of 35% in 2016 to an average of 2% in 2018.

As a result, coral-feeding fishes consumed broader diets (i.e., took bites from more coral species). Specifically, as coral cover decreased, so did the strength of fishes' dietary preferences (Fig. 3.2B., GAMM coral covariate: $t = 14.24$, $p < 0.001$). Fish species also differed significantly in their overall strength of dietary preferences ($df = 3$, Likelihood Ratio Test = 338.95, $p < 0.001$). Both at low and high levels of food availability, *Chaetodon plebeius* had the weakest preferences (Preference Coefficient estimate: 0.492) with the other fish species exhibiting sequentially stronger coral preferences (*C. lunulatus*: 0.533, *C. citrinellus*: 0.598, *C. trifascialis*: 0.704). These values specifically reflect the strength of preferences among coral prey. The alternate GAMM, with the addition of an interaction between coral cover and species was not preferred via AIC ($\Delta AIC = 2.78$).

3.4.2 Evenness of fish diets given altered coral assemblages

Fish diets also became more even after bleaching (Figure S3.2, Kruskal-Wallis: $df = 2$, $X^2 = 11.30$, $p = 0.004$), despite no substantial change in the evenness of coral assemblages (Kruskal-Wallis: $df = 2$, $X^2 = 2.62$, $p = 0.270$). On average, fish diets increased in evenness by 10%. PIE (probability of interspecific encounter) differed between 2016 and both post-disturbance years (2017–- Dunn: $z = -3.14$, $p < 0.001$, 2018 – Dunn: $z = -2.63$, $p = 0.004$) but PIE did not differ between 2017 and 2018 (Dunn: $z = 0.452$, $p = 0.326$).

3.4.3 Influence of disturbance on niche partitioning among coral-feeding fishes

More generalized diets among foragers were associated with a decrease in resource overlap, with all species decreasing their focus on *Acropora* and instead consuming other genera. Prior to coral bleaching, resource use was significantly more overlapping than random (Fig. 3.3, SES = 2.20, $p = 0.041$). However, after bleaching (i.e., in 2017 and 2018) resource use no longer differed from a null expectation of random resource use (Fig. 3.3, SES = 1.37, $p = 0.097$).

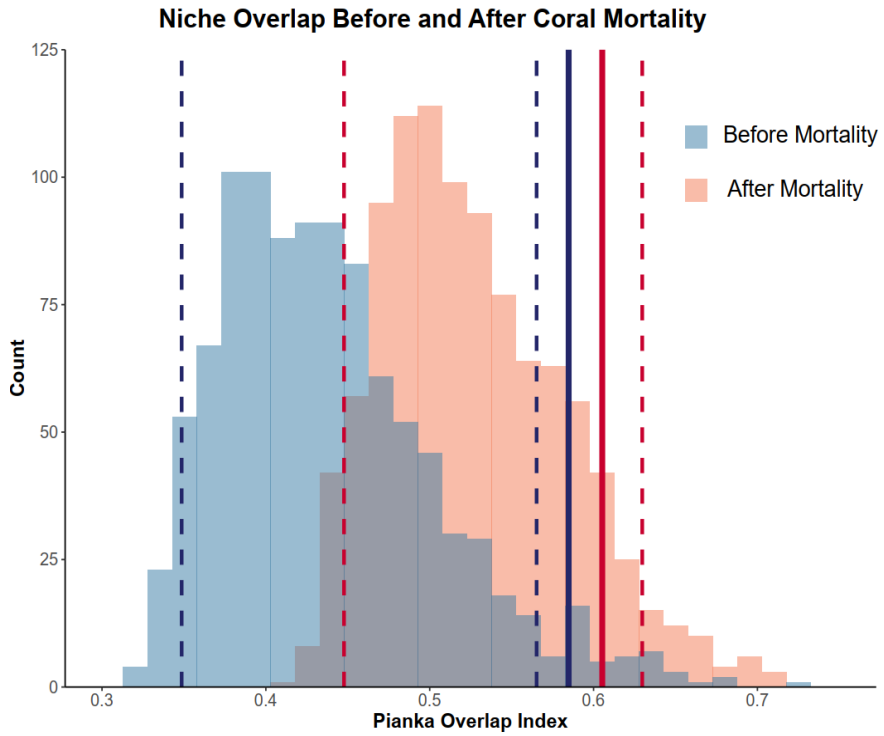

Figure 3.3 Null model analysis of resource partitioning with EcoSim before (blue, 2016) and after (orange, 2017 + 2018) coral mortality. Null matrices were generated with algorithm "RA3". Solid vertical lines represent the Pianka overlap index measured before and after disturbance, histograms represent the null expectation for each disturbance condition, and dashed vertical lines represent the 95% CI for the null expectation.

3.4.4 Change in forager networks following disturbance

Disturbance led to structural changes in interaction networks (Fig. 3.4). Specifically, networks were 11% more connected, 29% more even and 17% less specialized after the disturbance (Table S3.3). Probability distributions of interaction networks were significantly different before and after disturbance (KS: $D = 0.081$, $p = 0.006$). Shannon diversity (16%) and nestedness of networks (5%) increased as well. Prior to bleaching (2016), evenness of interactions was significantly greater than the null expectation (Fig. S3.3A, SES = 3.14, $p = 0.001$). Evenness continued to be higher than expected after disturbance, though the effect was marginally non-significant (2017 + 2018, SES = 1.29, $p = 0.097$). Diversity of interactions was significantly less than the null expectation in 2016

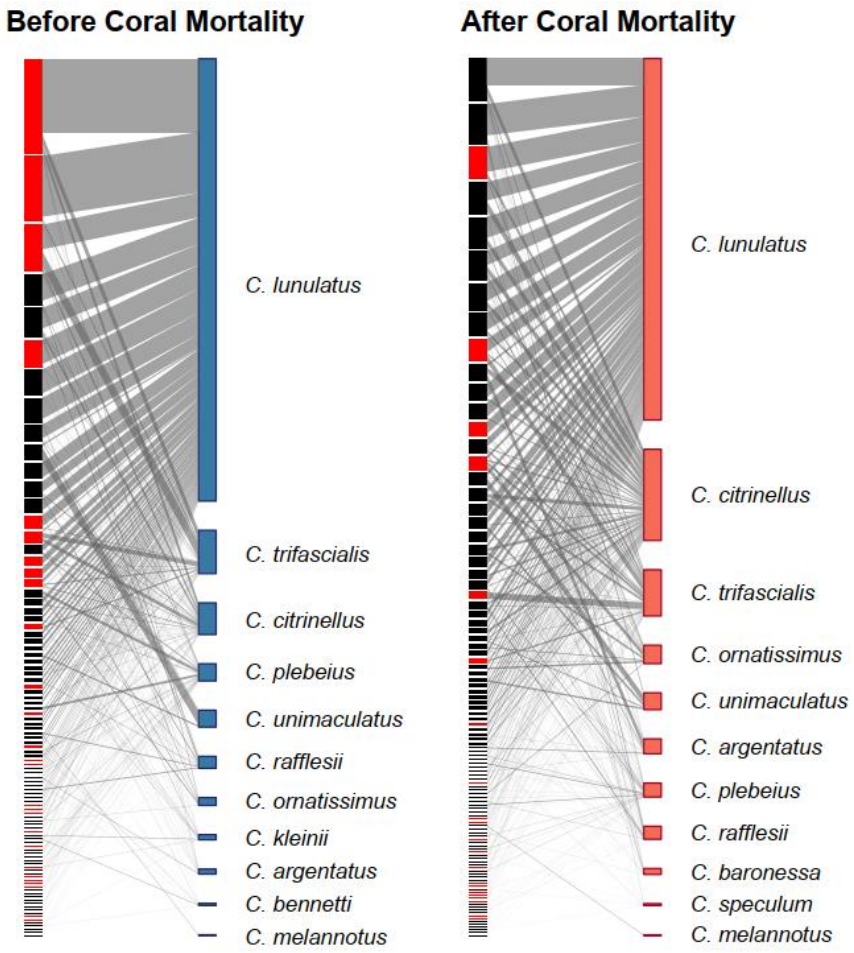

Figure 3.4 Visualization of foraging network structure before (blue, 2016) and after (orange, 2017 + 2018) coral mortality. The width of right bars represents the number of bites observed for each fish species; the width of left bars represents the number of bites taken on each coral species. The width of each connection represents the number of bites taken by a given fish species, on a given coral species. Both coral and fish species are arranged by the total number of bites observed. Coral species shown with red bars are of the genus *Acropora*, which is highly susceptible to bleaching and is also a highly sought-after food resource for many butterflyfish. All other coral genera are colored in black.

(Fig. S3.3B, SES = -5.09, $p < 0.001$), however no longer differed from a null expectation after disturbance (2017 + 2018, SES = -0.98, $p = 0.163$).

These structural changes were accompanied with considerable change in the composition of interactions. A year after bleaching (2016 vs 2017), there was a notable change in interactions

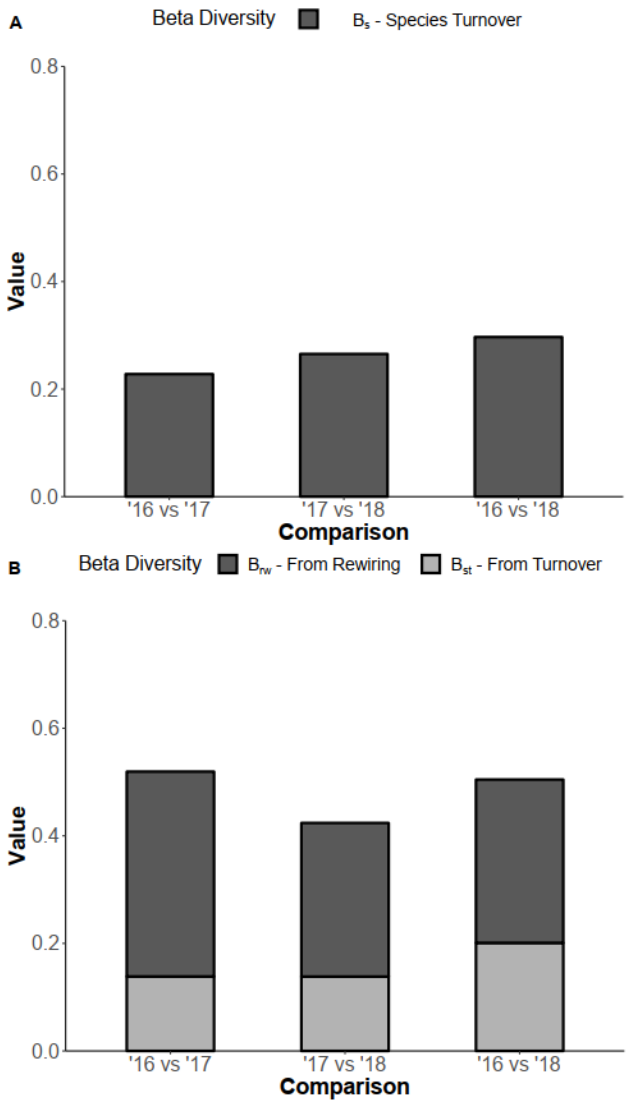

Figure 3.5 Interannual comparisons of network structure (temporal Beta diversity) for forager interactions. A) βs represents the difference in species presence (turnover) between years. B) βrw is the degree of difference in network structure due to interaction "re-wiring", whereas βst is the degree of difference in networks structure due to species turnover. Comparisons from left to right: 2016 vs 2017, 2017 vs 2018, and 2016 vs 2018. Please note that the bars on the left and the right are comparisons of before and after the coral mortality event whereas the middle bar compares between the two years after mortality.

(Fig. 3.5B, β_{int} = 0.519) with a large majority of this change due to interaction rewiring (73.3%, β_{rw} = 0.381). In the subsequent year (2017 vs 2018) the degree of species turnover remained as high as observed immediately after disturbance (Fig. 3.5A, β_s = 0.265 and 0.228, respectively);

additionally, interaction networks continued to change, however to a lesser degree (β_{int} = 0.424) and with a lower proportion of this change due to rewiring (67.4%, β_{rw} = 0.286).

3.5 Discussion

Our observations over three years of butterflyfish feeding show that bleaching-induced coral mortality is associated with behavioural changes in individuals that alter resource use among species and substantially restructure butterflyfish-coral interaction networks. After a coral bleaching event, coral cover decreased by 65%, resulting in butterflyfish altering the frequency of coral food items in their diet and weakening their dietary preferences, as predicted by ecological theory. For example, *Chaetodon trifascialis* previously took 37% of its bites from its preferred food source, *Acropora hyacinthus*—after bleaching, these corals only comprised 16% of its diet, with fish now consuming additional *Acropora* (38%) and *Montipora* (39%) species. Weakened dietary preferences resulted in less resource overlap at the genera level, with nearly all species lessening their consumption of bleaching-sensitive *Acropora* corals and increasing their consumption of other genera. The weakening of prey preferences seen here indicates that this is not simply a case of prey switching, and instead closely follows the niche expansion prediction within the optimal diet theory (Emlen 1966). Under a case of prey switching, species would shift their preferences onto those resources which have become most abundant, rather than weakening their ordered preferences altogether (Murdoch 1969, Cornell 1976). This does not appear to be the case here, with a breakdown of consistent hierarchies after the mortality event. Changing dietary preferences led to substantial changes in the structure of the consumer-resource interaction network, with much of this change due to interaction rewiring. Butterflyfish began to form new interactions, exploiting resources previously not considered, even among resources previously available (topological rewiring). They also altered the frequency of food items in their diet,

increasing their overall dietary evenness (interaction strength rewiring). Two years after disturbance, interaction networks have not returned to their initial configuration and continue to experience interaction rewiring.

All four species showed a weakening of preferences and, though they differed in their initial preference strength, degree of specialization, the magnitude with which their preferences weakened was similar. This pattern suggests that these species might have a similar capacity for plastic behaviour, which is intuitive given their shared environment and evolutionary history but comes at odds with some expectations regarding the evolution of generalist strategies and phenotypic plasticity. Both phenotypic plasticity and generalist strategies tend to evolve under exposure to heterogenous conditions (Kassen 2002, Stearns 1989). While previously thought to be homogenous environments, recent research has shown considerable variability in assemblage structure on coral reefs at and below the regional scale (Williams et al. 2015, Pawlik and Loh 2016). This, in addition to the substantial structural complexity of pristine reefs prior to human influence (Alvarez-Filip et al. 2009, Graham and Nash 2013), appears to support the evolution of both generalist strategies, and behavioural plasticity in this system. However, because the evolution of generalist strategies tends to coincide with the evolution of phenotypic plasticity (van Tienderen 1997), there is some expectation that generalists could have a greater degree of innate plasticity. Another possibility in this system, however, is that specialist species might have to alter their diet to a greater extent, as the corals that specialist butterflyfishes fed upon are also some of the most susceptible to bleaching-induced mortality (Marshall and Baird 2000, Loya et al. 2001). In this case, neither expectation was clearly met as generalist butterflyfishes did not show a different degree of behavioural change than their specialist counterparts.

In addition to reflecting the flexibility of these fish, their ability to form new connections with other coral species undoubtedly also reflects functional similarities among remaining coral species (Schleuning et al. 2020). The likelihood of any pair of species to interact depends on a series of matching traits, which may be morphological, physiological or chemical (Bartomeus et al. 2016). Proposed efforts to predict interaction changes based on functional traits appear promising. In this case, the likelihood of forming new interactions could be limited by the shape of coral growth forms (Hughes 1987, Madin et al. 2016), the gape width of butterflyfish species (Konow and Ferry 2014), inducible defense traits like nematocyst density (Gochfeld 2004), or by the production of essential nutrients by corals (Brooker et al. 2013).

The shifting of foraging efforts off of *Acropora* onto different genera led to a reduction in resource overlap among species at the genera level. This reduction of overlap indicates that while dietary preferences became weak, species still partitioned the remaining resources to a greater degree than they did before mortality, coinciding with previously documented reductions in inter-specific aggression (Keith et al. 2018) This raises interesting questions for the future of this system, and the long-term effects of coral mortality on butterflyfish abundance and survival. Our results show butterflyfish are surprisingly flexible in their diet selection in the short term, however bleaching-induced coral mortality has a profound and long-lasting effect on food availability in this system. Estimates of recovery time for a bleached reef range from 7-29 years without disturbance (Gouezo et al. 2019, Robinson et al. 2019). In contrast, bleaching events have become a frequent occurrence, with the average bleaching recovery window shortening from 27 years in the early 1980s to six years in 2016 (Hughes et al. 2018). Will this partitioning persist in the long term, even if coral populations don't recover? And in light of this partitioning, how will populations respond? Butterflyfish population sizes have been seen to decline substantially following coral mortality,

particularly among obligate coral-feeders (Wilson et al. 2013), and fish that do persist may still face sublethal effects of reduced body condition (Pratchett et al. 2004, see **Chapter 4** for more details on their the possible causes and consequences). However, while populations are expected to decline, the broad flexibility developed by these fish may play an important factor in species persistence in the long term. Understanding dietary changes among butterflyfish species is an important step in determining their relative competitive ability, which will aid in predictions of species persistence under continued change. Continued monitoring of butterflyfish feeding and population sizes will be performed at these sites and should help to shed light on how their resource use and competitive abilities will evolve.

Continued changes in consumer-resource interactions at these sites raise questions about the temporal variation of interaction network structure. Namely, how closely is network structure tied to habitat condition? Two years after this disturbance event, consumer-resource interactions have not returned to their initial condition and have continued to experience year to year variation on a similar scale. If reefs are able to return to their initial coral cover, will interactions also return to their pre-disturbance configurations? And if so, what is the lag between reef recovery and behavioural responses? Conversely, it is possible that interaction structure will return to a condition similar to its initial state, without complete recovery of the habitat. This would be possible if another coral increases in relative abundance and consumption, replacing *Acropora* as the dominant food resource.

One important factor in the future and persistence of these altered interaction networks is their robustness to species extinctions. The robustness of ecological networks is an emergent phenomenon seen to coincide with certain aspects of network topology, such as high connectance and nestedness (Dunne et al. 2002) and is typically measured by simulating the response of

networks to random extinctions (Borvall et al. 2000). Here, both connectance and nestedness of consumer-resource networks increased following disturbance. These offer some hint that these networks could have increased in robustness following disturbance. While this would indicate that these networks may be more stable in this post-mortality state, it does not preclude the possibility of further change in this system, particularly given the substantial flexibility shown by these fish.

In conclusion, behavioural responses to anthropogenic disturbances can have wide-reaching impacts on species interactions and overall community structure. Coral mortality following bleaching is one of many human-induced disturbances that can bring about drastic shifts in foraging behaviour (Samways 2005, Keith et al. 2018, Thompson et al. 2019). This work illustrates highlights an existing response pathway for community change, whereby a reduction in food availability affects the structure of interaction networks through changes in dietary specificity and overlap. For corallivores, coral mortality caused a major decrease in food supply and weakened dietary preferences. This simultaneous dietary expansion of multiple species occurred in such a way that all species reduced their consumption of bleaching-sensitive *Acropora*, instead consuming a variety of other coral genera, and resulting in decreased resource overlap. Changing dietary preferences also led to substantial rewiring of the consumer-resource interaction network. This set of responses could prove particularly informative for disturbances in other systems structured by bipartite interaction networks, such as plant-pollinator systems. To better understand and manage the effects of disturbance events, we must consider how the influence on animal behaviour, which can have a profound influence on species interactions and restructure ecological communities.

3.6 Chapter Acknowledgements

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3.7 Contribution of Authors

RFS, AHB, and SAK proposed dietary analysis methods. NJS and PJC proposed network and community analysis methods and supervised their usage. RFS performed all data analyses and wrote the first draft of the manuscript, all authors contributed substantially to revisions. AHB collected all foraging observation / coral cover data. JPWR and XJ assisted with model fitting and community analyses.

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4. Divergent foraging behaviour in coral reef fishes associated with resource availability

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Robert F. Semmler[1], Nicholas A.J. Graham[1], Nathan J. Sanders[2], Andrew H. Baird[3], Sally A. Keith[1]

[1]Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, UK

[2]Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, 05405, USA

[3]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, 4811, Australia

4.1 Abstract

Anthropogenic disturbance of food availability can alter a variety of aspects of animal behaviour (i.e., bottom-up effects), including foraging behaviour. How species forage in low-food environments can provide important insight into their potential response to food disturbance, and responses to low-food conditions may be expected to differ between specialists and generalists. We investigated how the foraging behaviour of coral-feeding butterflyfishes varies across a gradient of habitat conditions, whether variations follow predicted responses from optimal foraging theory, and whether there are notable differences between specialist and generalists. We found that species vary multiple aspects of their foraging behaviour in low-coral environments. The most notable of these differences was for the specialist, *C. trifascialis*, which normally displays territorial behaviour, but instead showed roaming behaviour in low-coral environments, with lower patch residence times in these areas. This response was not shared by the other generalist species. Despite this variation in behaviour, however, the species had lower overall bite rates in low-coral areas. This, in addition to the lower nutritional quality of non-preferred food sources may drive observed population declines after coral bleaching events. This indicates that specialist species may be capable of shifts in foraging behaviour in the short-term, whilst remaining vulnerable to the largest population declines in the longer-term.

Keywords: *resource availability, optimal foraging, specialization, patch-residence, bite rate*

4.2 Introduction

Anthropogenic disturbance causes substantial change to ecosystems across the globe, including modifying habitats, and altering species compositions (Vitousek et al. 1997, Barnosky et al. 2012). These changes can profoundly affect animal behaviour (Wilson et al. 2020). One of the most common ways disturbance alters animal behaviour is through changes in food availability (i.e., bottom-up effects, Wilson et al. 2020). Habitat degradation, for example deforestation or coral reef bleaching, can drastically reduce food supply (Heiduck 2002, Pangau-Adam 2015, Wilson et al. 2014, Keith et al. 2018), which can lead to changes in the foraging behaviour of consumers (Tuomainen and Candolin 2011).

Foraging behaviour is the product of countless decisions that are made by individuals to optimize energetic gain (Schoener 1971). Optimal foraging decisions reflect the habitat conditions in which those decisions are made and, as such, foragers may make different foraging decisions in response to changing habitat conditions (Snell-Rood 2013). Likewise, average foraging traits (e.g., average patch residence time, bite rate) reflect the baseline propensity to make certain decisions and should vary in response to habitat conditions. For instance, average patch residence time, bite rate, and movement duration can change as food availability changes (Krebs et al. 1974, Charnov 1976), and the extent of these changes might be expected to differ between specialists and generalists. While specialist species face greater risk of local extinction from disturbance (McKinney 1997, Devictor et al. 2008), less is known about how specialists and generalists forage in low-food conditions and how differences in foraging behaviour in low-food conditions might inform their relative degree of behavioural response to disturbance.

Here, we test the extent to which the foraging behaviour of coral-feeding butterflyfishes varies spatially over fine scales, with varying levels of food availability. We also evaluate how closely

these behavioural differences follow predicted responses from optimal foraging theory. Specifically, we quantify how four foraging traits (patch residence time, bites per foray, bites per patch, movement duration) vary across habitats along a gradient of food availability, and whether behavioural differences with varying food availability are consistent among both specialist and generalist species. We do this through direct observations of foraging behaviour on reefs with different levels of coral cover. Specifically, we test the hypothesis that fish in low-coral territories compensate for lower food availability with a higher instantaneous bite rate (Penning 1986), increased patch residence time, and more bites per patch. Fish with longer patch residence times will also tend to make longer foraging movements, consistent with the marginal value theorem (Charnov 1976). Lastly, we also explore how differences in these foraging behaviours affect the overall bite rate, and whether fishes in low-coral territories maintain a similar overall bite rate to individuals in high-coral territories. We ask to what extent: 1) coral cover or variation in coral cover predict the four foraging trait values, 2) the relationship between coral properties and foraging traits can be predicted by individual species identity, focusing on differences between the specialist *C. trifascialis* and three other species, and 3) coral cover / variation in coral cover can predict the overall bite rate of these species.

4.3 Methods

4.3.1 Data collection

We collected data on four butterflyfish foraging traits through observations of coral cover and fish behaviour at four reefs in the Ryukyus Islands, Japan in July 2018. We sampled three reefs off the island of Iriomote (14-19th July 2018), in the southern Ryukyus (Fig. 4.1): Nata (24.43 N, 123.79

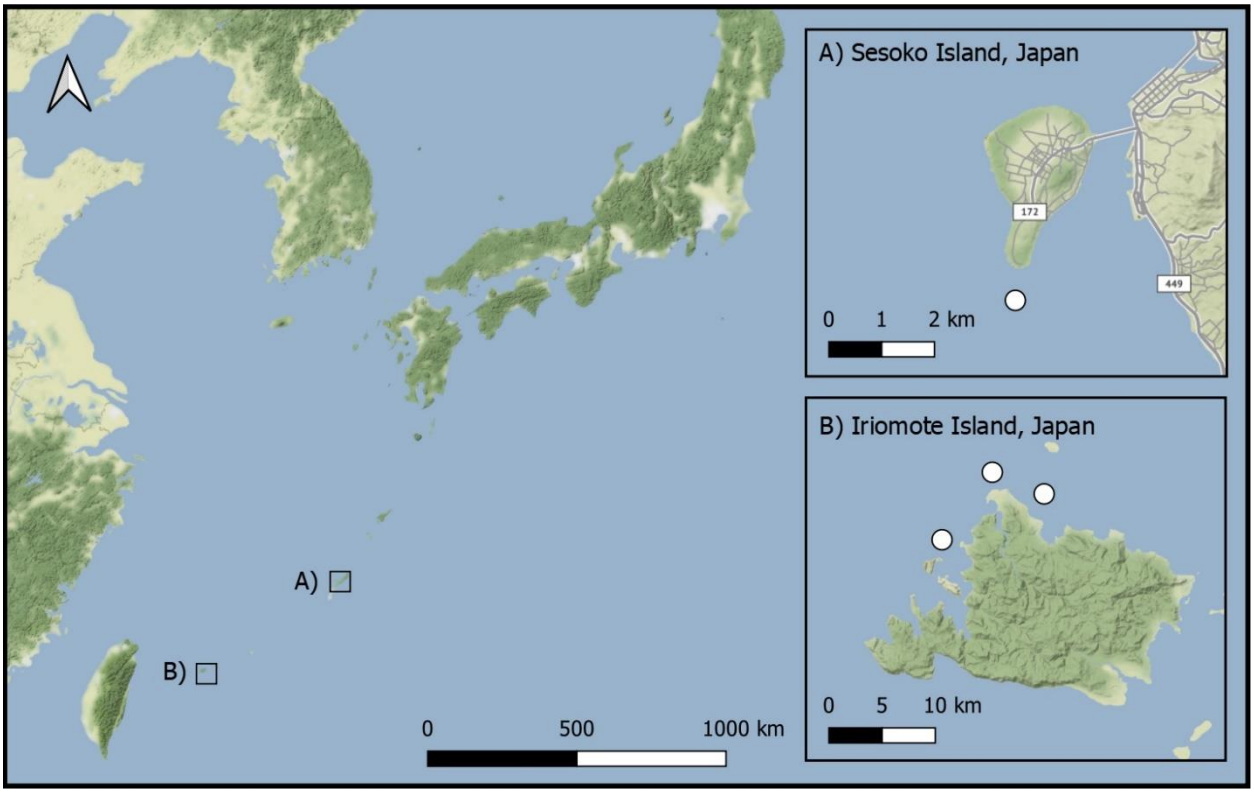

Figure 4.1 Map of the Ryukyus Islands, Japan, with insets of A) Sesoko (above) and B) Iriomote (below). The white dots indicate the four reefs locations where foraging behaviour was recorded.

E), Sonai (24.38 N, 123.75 E), and Unarizaki (24.43 N, 123.76 E), and one reef off the island of Okinawa (July 21-22nd 2018) in the central Ryukyus (Sesoko Point, 26.63 N, 127.86 E). In May and June of 2016, the three reefs off Iriomote experienced substantial bleaching and mortality as a result of the 2016 global coral bleaching event–- within a year of the bleaching event, the three Iriomote reefs had experienced an average coral mortality of 65% (Baird et al. 2018, Keith et al. 2018). In contrast, Sesoko Point experienced only minor bleaching among a specific subset of *Acropora* corals (<10% of digitate *Acropora* colonies) with no change in the overall coral mortality rate from pre-bleaching levels(Singh et al. 2019). By the time of behavioural sampling, Iriomote reefs averaged 24% hard coral cover (±S.D. 10%), whereas Sesoko Point averaged 68% coral cover (±S.D. 9%).

4.3.2 Foraging behaviour

We observed four butterflyfish species, which reflected a broad spectrum of feeding strategies and degrees of reliance on hard coral: *Chaetodon trifascialis* is a highly specialized obligate corallivore which, prior to bleaching in Iriomote, took 93% of its bites from *Acropora* corals, with 59% specifically from large tabular *Acropora* spp. (see **Chapter 3**); *Chaetodon lunulatus* is also an obligate coral-feeder but is more generalist in its coral consumption, taking 51% of its bites from *Acropora* and 22% specifically from tabular *Acropora* spp. (see **Chapter 3**); and *C. ephippium* and *C. vagabundus* are occasional coral-feeders (i.e., facultative corallivore and invertivore, respectively, Cole and Pratchett 2014), neither of which specializes on particular corals. These four species were also abundant on all four reefs (account for 62% of butterflyfish sightings), allowing us to gain sufficient sample sizes for each despite the relatively low abundance of butterflyfish in general on degraded reefs.

To record foraging traits, we followed focal fish on snorkel and video recorded their foraging for five minutes each with an underwater camera at 30 frames per second (3 used: 1) Canon PowerShot G7 X Mark II at 1080p, 2), Canon PowerShot D30 at 480p, 3) Olympus TG-5 at 720p). Butterflyfish are typically undisturbed by diver presence (Kulbicki 1998) and we also minimized effects of the observer by preceding each five-minute observation with a separate one-minute acclimation period to ensure the fish was responding naturally (i.e., feeding). During the observation, the observer maintained a distance greater than the fish's perceived flight initiation distance (FID; 2-4 m) and minimized movement. If the fish moved out of frame (e.g., underneath a coral colony) for longer than 30 sec, the observer extended the observation to record five minutes of fish activity within frame. On rare occasions a full five minutes could not be completed if the fish moved out of frame and could not be relocated. These observations were only used if they

were at least four minutes in length. This accounted for four of the 95 observations in the analysis and average time in frame for these observations was similar to those recorded for a full five minutes. Many butterflyfish species are pair-forming so to avoid dependence in our observations, only one member of a given pair was observed. To avoid repeat sampling of the same fish, the observer found each subsequent focal fish by travelling along the reef flat and crest in a U-shape search pattern (Chidlow et al. 2006). Contextual variables of date, time, and wave conditions were recorded for each observation.

4.3.3 Coral cover

We quantified territory-level coral cover directly from foraging videos. Territory-level coral cover was preferred over other site-level measures because this better reflected the local habitat information used to make foraging decisions and captured the variability in territory-level coral cover within sites. A single observer (RFS), paused videos within VLC Media Player at specific time intervals and estimated the percentage of hard coral cover within the frame to the nearest 5%. Direct corals ID's were not made. Visual estimates of coral cover and habitat complexity tend to perform very similarly to transect based methods (Wilson et al. 2007). Five assessments were made for each video (at 30 s, 1 min 30 s, 2 min 30 s, 3 min 30 s, 4 min 30 s). If the frame these intervals selected was not sufficiently clear (e.g., due to diver movement following the fish) the observer moved forward frame by frame until the next clear view. In cases where the foraging observation was cut short, or lasted longer than 5 min, assessment intervals were shifted to be evenly spaced within the feeding observation.

4.3.4 Extracting traits from foraging videos

To extract relevant behavioural data from foraging videos we used the program BORIS (Friard and Gamba 2016) following a similar methodology to Zambre et al. (2018). Videos were uploaded and a single observer (RFS) watched each at slow (0.6x) speed, marking when the fish started/stopped feeding, moving, or engaged in aggressive behaviour, as well as any time the fish was out of frame. Forays, or individual foraging bouts, were defined by a head-down orientation, and ended when the fish elevated its head from the substrate by greater than 45° (Nash et al. 2012). Multiple consecutive forays often occurred in the same location. Forays within ≤ 1 m of each other were designated to be in the same patch. Accordingly, forays within the same patch occurred back to back, whereas forays in differing patches were separated by a bout of movement. The same observer then watched through the same video at higher (0.8x) speed, recording every bite the fish took on the benthic substrate. It should be noted that bites on the benthic substrate will not be limited to consumption of corals, as this distinction cannot be made without more invasive methods Each video was then watched by the same observer a third and final time for quality control to confirm, and if necessary, adjust the data.

Video output files were imported into R and we calculated:

1. Patch Residence Time, or the time spent feeding in a given patch, which captured the time between the start and end of each set of consecutive forays
2. Movement Duration which was the time between the start and end of each movement bout
3. Bites per Patch which was the number of bites taken within each set of consecutive forays

4. Bites per Foray which was the number of bites taken within each head-down foraging bout

For each of these traits, we recorded multiple values for each individual. Additionally, to illustrate how varying these four behaviours might influence the total number of bites taken, we also calculated an overall feeding rate for each individual, using the total number of bites per unit time the individual was in frame. However, it should be noted that, as we do not have nutritional information for the corals consumed, this will not be representative of overall energy intake.

4.3.5 Data analysis

To answer our questions, we used a common set of *a priori* candidate models with an information criterion (IC) approach. We use one set of these models to predict each of the four foraging traits, and an additional set to predict the overall feeding rate. In these models, coral cover and variation in coral cover are discrete predictors, and fish species is a categorical predictor. All models were run with package "lme4" (Bates et al. 2015). If two models differed by 2 or less in AIC, then the simpler model was preferred (Richards 2005). The general structure for the candidate models is as follows:

Model 1: Trait ~ Coral Cover + Variation in Coral Cover + Fish Species

Model 2: Trait ~ Coral Cover + Fish Species

Model 3: Trait ~ Coral Cover * Fish Species

Model 4: Trait ~ Fish Species

Model 5: Trait ~ Intercept Only

4.3.6 Effects of resource availability on four foraging traits

For each of the four foraging traits we used a set of generalized linear mixed effect models (GLMMs). As there are multiple observations of each foraging trait for a given individual (e.g., multiple forays or movement bouts), there was dependency among these observations. To account for this dependency, we used fish identity as a random effect, with a fixed slope and a varying intercept. It was hoped that both coral cover and variation in coral cover might be uniquely informative, however, during model fitting it was determined that the two were significantly collinear ($cor = 0.421$, $t = 4.57$, $p < 0.01$).

The model type used for each trait depended on the properties of the predicted values (discrete vs continuous etc.) and the optimal model type was determined via dispersion values closest to 1. For patch residence time and movement duration we used Gamma GLMMs, for bites per patch we used negative binomial GLMMs, for bites per foray we used Poisson GLMMs. For question 1 of our analysis, our hypothesis was supported for any of the four foraging traits if the optimal model selected for that trait included coral cover or variation in coral cover. For question 2, our hypothesis was supported for any of the traits if the optimal model included an interaction between coral cover and fish species. For all GLMMs, we predicted the given trait along the range of observed coral cover for each species. We generated 95% confidence intervals around these predictions using jackknife resampling, whereby we randomly subset the dataset to 80% of the observations, re-fitted the model and generated predictions on this subset, and repeated the process for 100 replicates (McIntosh 2016). These 100 jackknife predictions were ordered, and confidence

intervals taken as the 5^{th} and 95^{th} values. Predictions were made specifically on one level of the random intercept effect.

Lastly, one concern in this approach is that comparisons of varying food availability are made both within and across sites. To ensure that site-level properties don't influence these results, we also employ an alternate set of models (detailed in Supplemental Info) which focused solely on the variance in foraging traits within sites. These were not used for the formal analysis because the inclusion of multiple random effects led to overfitting concerns and difficulties with model convergence, however they provide important insight into potential mechanisms for behavioural variation and illustrate that site effects should be minimal.

4.3.7 Overall bite rate

To answer question 3 of our analysis, we compare the same set of candidate models above, for the overall feeding rate. As there was only a single overall feeding rate for each individual fish, no random effects were included in these models. As before, model type was chosen based on a dispersion closest to 1. For overall feeding rates, we used gamma GLMs. For question 3, our hypothesis was supported if the optimal model for the overall bite rate included coral cover or variation in coral cover. For this GLM we predicted the overall bite rate along the range of observed coral cover for each species, calculating variance around these estimates within 2 standard errors.

4.4 Results

We recorded foraging behaviour for a total of 99 individuals, and for a total duration of 373 minutes in frame (Table 4.1). Results of model fitting are listed in Table 4.2.

Species	n (Total)	n (Sonai)	n (Nata)	n (Unarizaki)	n (Sesoko)	Dietary Category	Specialized on *Acropora*
Chaetodon ephippium	18	6	8	4	0	Facultative Corallivore	No
Chaetodon lunulatus	29	7	6	9	5	Obligate Corallivore	No
Chaetodon trifascialis	23	6	7	3	7	Obligate Corallivore	Yes
Chaetodon vagabundus	29	8	7	7	5	Invertivore	No

Table 4.1 Butterflyfish species included in this analysis, and the total number of each video recorded. Dietary designations taken from Cole and Pratchett 2014.

4.4.1 Effects of resource availability on four foraging traits

Patch residence time varied 1.5-fold among species (LR Test: $X^2 = 13.25$, $p = 0.004$), and there was an interaction between species identity and coral cover (Fig. 4.2A, LR Test: $X^2 = 10.81$, $p = 0.013$). *Chaetodon ephippium* and *C. vagabundus* in low-coral territories spent more time in a given patch (est = -0.68 sec per 10% coral cover and -0.33 sec per 10% coral cover, respectively), whereas *C. trifascialis*, the specialist coral-feeder, showed the opposite effect, spending less time in a given patch in lower coral cover territories (est = 0.53 sec per 10% coral cover). Overall, *C. ephippium* had the longest patch residence time on average (Fig. 4.3A, model estimate = 7.07 sec, 95% CI: 5.96 – 8.19 sec), spending more time in a given patch than *C. vagabundus* (5.36 sec, $p = 0.011$, 95% CI: 4.63 – 6.09 sec) and *C. trifascialis* (4.72 sec, $p < 0.001$ 95% CI: 3.88 – 5.56 sec). *Chaetodon ephippium* did not spend significantly more time in a given patch than *C. lunulatus* (6.17 sec, $p = 0.107$, 5.44 – 6.91 sec).

Bites per foray decreased by 0.05 per 10% coral cover (Fig. 4.2B, 95% confidence intervals (C.I.): -0.10 to -0.01), meaning fish in lower coral cover territories took a greater number of bites during

Trait	Candidate Model	AIC
Residence Time	Time ~ Coral + Variation in Coral + Species	8853.8
	Time ~ Coral + Species	8853.9
	Time ~ Coral * Species	**8849.1**
	Time ~ Species	8855.1
	Time ~ Intercept Only	8860.2
Movement Duration	Time ~ Coral + Variation in Coral + Species	12134.0
	Time ~ Coral + Species	12132.9
	Time ~ Coral * Species	12130.5
	Time ~ Species	**12131.2**
	Time ~ Intercept Only	12142.1
Bites Per Foray	Bites ~ Coral + Variation in Coral + Species	8720.1
	Bites ~ Coral + Species	**8721.0**
	Bites ~ Coral * Species	8722.5
	Bites ~ Species	8725.7
	Bites ~ Intercept Only	8852.0
Bites Per Patch	Bites ~ Coral + Variation in Coral + Species	6644.5
	Bites ~ Coral + Species	6644.6
	Bites ~ Coral * Species	**6640.3**
	Bites ~ Species	6644.7
	Bites ~ Intercept Only	6736.2
Overall Bite Rate	Rate ~ Coral + Variation in Coral + Species	-214.0
	Rate ~ Coral + Species	-210.7
	Rate ~ Coral * Species	**-220.6**
	Rate ~ Species	-212.5
	Rate ~ Intercept Only	-173.8

Table 4.2 Candidate models posed for each question. Traits highlighted in gray indicate the null hypothesis for the given question was rejected. Bolded AIC values indicate the most appropriate model for each comparison. If two models differed by 2 or less in AIC, then the simpler model was preferred. Traits highlighted in light gray varied significantly with coral cover. Traits highlighted in dark gray showed an interaction between coral cover and fish species.

each "head-down" feeding bout. Bites per foray varied nearly threefold among species (Fig. 4.3B, LR Test: $X^2 = 134.77$, $p < 0.001$), but there was no interaction between coral cover and species identity (LR Test: $X^2 = 4.55$, $p = 0.207$). *Chaetodon ephippium* took the most bites per foray (model estimate = 2.50 bites, 95% CI: 2.24 – 2.79 bites, *C. lunulatus*: 2.14 bites, $p = 0.028$, 95% CI: 1.97 – 2.33 bites, *C. trifascialis*: 1.17 bites, $p < 0.001$, 95% CI: 1.04 – 1.30 bites, *C. vagabundus*: 0.85 bites, $p < 0.001$, 95% CI: 0.76 – 0.95 bites).

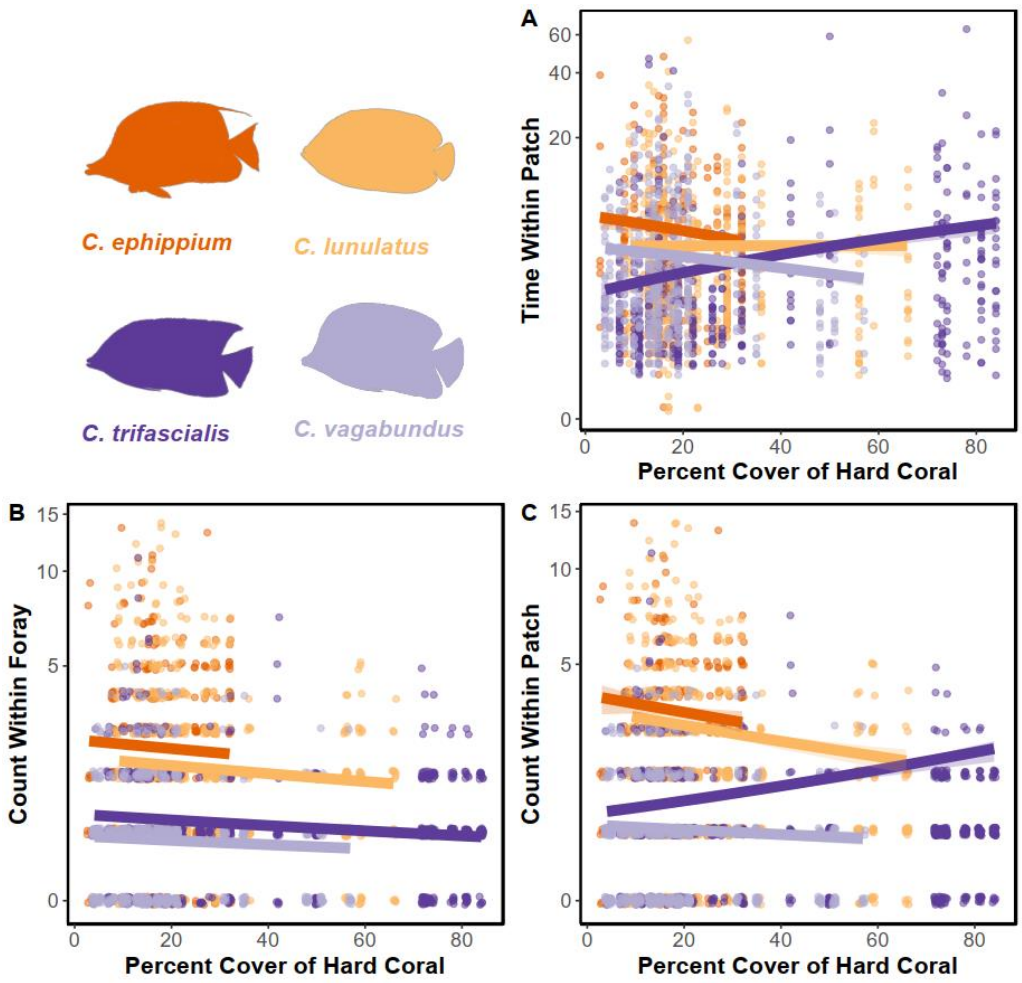

Figure 4.2 Linear models of foraging traits which responded to varying coral cover. Confidence intervals around predictions were made using jackknife resampling of 80% of the entire dataset. Predictions are made specifically on one level of the random effect (Subject = EPH001). A) Effect of hard coral cover on patch residence time. B) Effect of hard coral cover on the number of bites per foray. C) Effect of hard coral cover on the number of bites per patch.

Bites per patch varied more than threefold among species (LR Test: $X^2 = 97.56$, $p < 0.001$) and there was an interaction between coral cover and species (Fig. 4.2C, LR Test: $X^2 = 10.30$, $p = 0.016$). *Chaetodon ephippium, C. lunulatus*, and *C. vagabundus* in low-coral territories took a greater number of bites per patch (est = -0.14 bites per 10% coral cover, and -0.13 bites per 10% coral cover, and -0.04 bites per 10% coral cover, respectively), whereas the specialist, *C.*

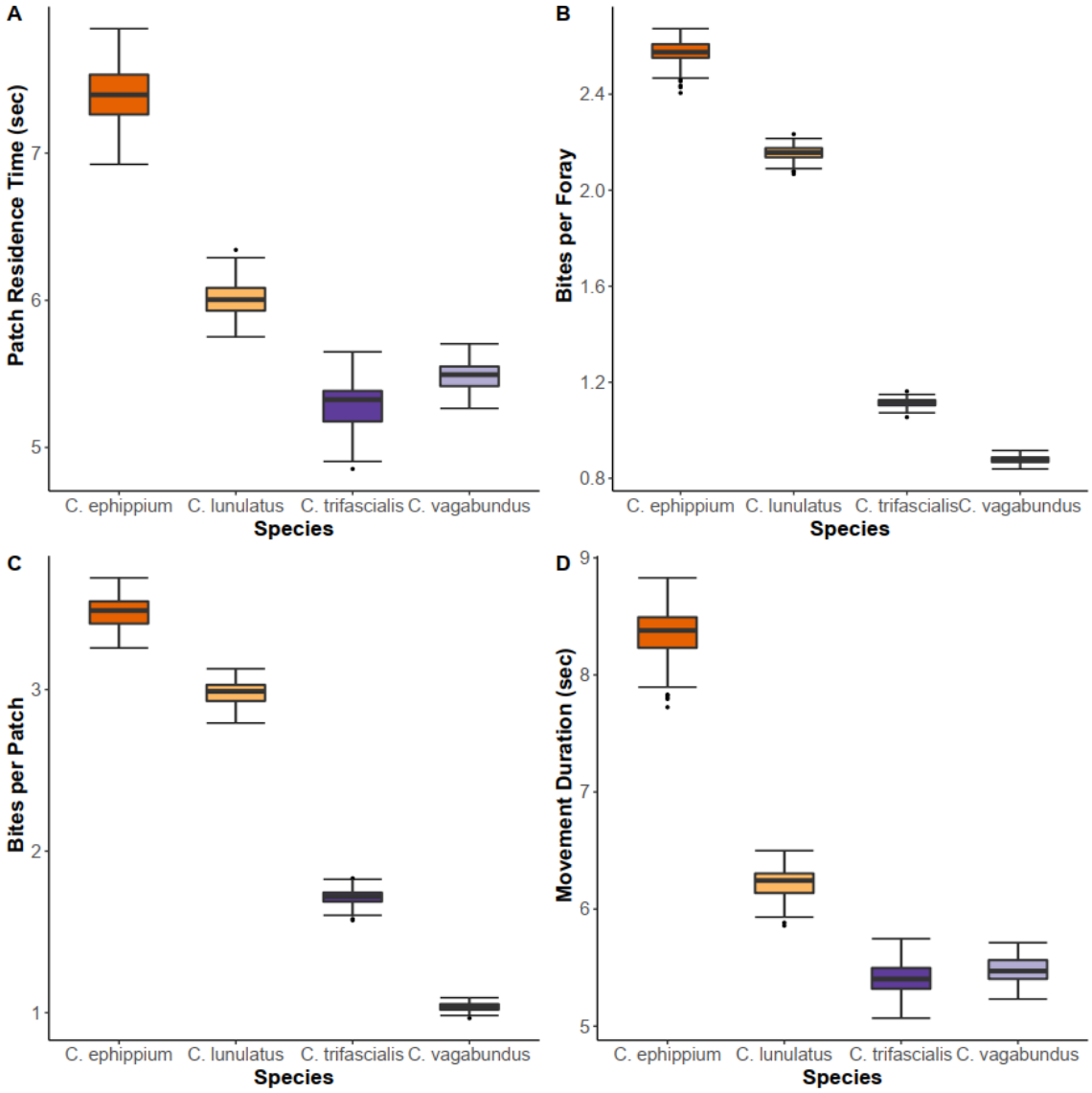

Figure 4.3 Boxplots of foraging traits which varied with fish species. Error bars were generated using jackknife resampling of 80% of the entire dataset. Predictions are made specifically on one level of the random effect (Subject = EPH001). A) Effect of species on patch residence time, B) Effect of species on movement duration. C) Effect of species on the number of bites taken per foray. D) Effect of species on the number of bites taken within a patch.

trifascialis, showed the opposite effect, taking fewer bites per patch in low-coral territories (est = 0.12 bites per 10% coral cover). *Chaetodon ephippium* took the most bites per patch (Fig. 4.3C, model estimate = 3.37 bites, 95% CI: 2.81 – 4.04 bites), taking significantly more than *C. trifascialis* (1.55 bites, $p < 0.001$, 95% CI: 1.33 – 1.81 bites) or *C. vagabundus* (1.02 bites, $p <$

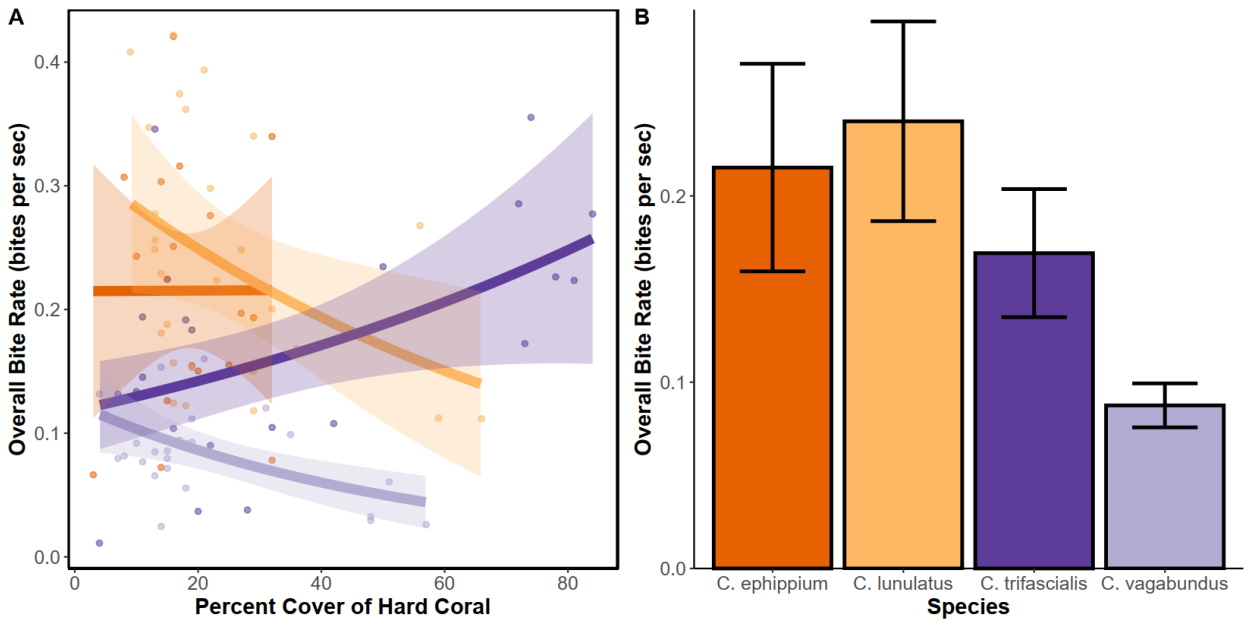

Figure 4.4 Effects of hard coral cover and fish species on overall feeding rate. Confidence intervals around predictions are two standard errors from the model mean. A) Effect of hard coral cover on overall bite rate. B) Effect of fish species on overall bite rate.

0.001, 95% CI: 0.88 – 1.17 bites). Bites per patch for *C. ephippium* did not differ significantly from *C. lunulatus* (est = 3.03 bites, p = 0.269, 95% CI: 2.65 – 3.36 bites).

For movement duration, coral cover was not included in the optimal model. Movement duration did, however, vary 1.5-fold among species (Fig. 4.3D, LR Test: $X^2 = 16.93$, $p > 0.001$). *Chaetodon ephippium* had the longest movement durations (model estimate = 8.47 sec, 95% CI: 7.25 – 9.70 sec), with each other species making significantly shorter movements on average (*C. lunulatus*: 6.27 sec, p = 0.004, 95% CI: 5.36 – 7.17 sec, *C. vagabundus*: 5.55 sec, $p < 0.001$, 95% CI: 4.66 – 6.44 sec, *C. trifascialis*: 5.48 sec, $p < 0.001$, 95% CI: 4.53 – 6.43 sec).

4.4.2 Overall bite rate

Overall feeding rates varied over 2.5-fold among species (LR Test: $X^2 = 29.06$, $p > 0.001$), and there was an interaction between coral cover and species (Fig. 4.4A, LR Test: $X^2 = 21.22$, $p > 0.001$). *Chaetodon lunulatus* and *C. vagabundus* in low-coral territories had a higher overall bite rate (est = -1.54 bites/min per 10% coral cover, and -0.90 bites/min per 10% coral cover, respectively), whereas the specialist, *C. trifascialis*, showed the opposite effect, taking substantially fewer bites in low-coral territories (est = 0.94 bites/min per 10% coral cover). For *C. ephippium* there was virtually no difference in overall bite rate with varying coral cover (0.02 bites/min per 10% coral). *Chaetodon lunulatus* had the greatest feeding rate (Fig. 4.4B, est = 14.40 min^{-1}) taking significantly more bites per minute than *C. vagabundus* (est = 5.25 min^{-1}). The overall bite rate of *C. lunulatus* did not differ significantly from *C. ephippium* (est = 12.91 min^{-1}) or *C. trifascialis* (est = 10.16 min^{-1}).

4.5 Discussion

Under reduced food availability, both specialist and generalist species differed in foraging behaviour. In territories with low food availability, all species had higher instantaneous bite rates, consistent with predictions based on terrestrial grazer populations (Penning 1986, Iason et al. 1999). For traits specifically related to patch usage, behaviour varied substantially with territory-level coral cover, but with specialist *C. trifascialis* showing an opposite relationship from the three more generalist species. In low-coral cover areas, the infrequent or facultative coral-feeders had longer patch residence times and took more bites per patch, whereas *C. trifascialis* had substantially shorter patch residence times and took fewer bites per patch. These differences reflect the fact they also show alternate foraging patterns on healthy reefs.

Under normal conditions, *C. trifascialis* will establish small territories around its preferred prey (*Acropora* table corals), defending them from intruders (Pratchett 2005)–- a strategy often resulting in longer patch occupancy times (Stamps 1994, Adams 2001). In low-coral habitats however, these table corals are notably scarce, particularly following coral bleaching events. Before bleaching in 2016, average cover of *Acropora* corals in Iriomote was 35% across the three sites, whereas by 2018 average cover of *Acropora* was 2% (see **Chapter 3**). It is plausible that as a result of their low *Acropora* coral abundance, there is a lack of territoriality in low-coral habitats. Instead, *C. trifascialis* individuals in these territories display roaming behaviour, only occupying patches for a short period of time before moving on. *C. trifascialis* also had higher instantaneous bite rates within these areas, feeding faster on coral colonies when located. However, as a result of their shorter patch occupancy, the overall number of bites taken in a given patch is lower.

Chaetodon lunulatus is also an obligate corallivore but is more generalist in its coral consumption than *C. trifascialis*, consuming a wider variety of coral species (Pratchett 2004, Pratchett et al. 2005), many of which are not as strongly affected by bleaching as *Acropora* spp. are. Contrary to predictions, patch residence times for *C. lunulatus* were the same in low and high-coral territories. This may be because the species can feed on a large proportion of the species found in low-coral territories. However, while *C. lunulatus* didn't spend more time in a given patch in low-coral territories, it did take more bites from a given patch, as it increased its instantaneous rate in low-coral areas.

Chaetodon ephippium and *C. vagabundus* are infrequent coral-feeders, using corals to supplement their consumption of other benthic invertebrates (Pratchett 2005). Because corals form only a small portion of their diet, these two species were expected to show the least variation in behaviour along the gradient of coral cover. However, the two differ in some behaviours, with longer patch

residence times, and (like all other species) higher instantaneous bite rates in low-coral territories. One possible explanation is that these two have another option when faced with poor-quality coral patches so might target only coral patches with a guaranteed energy gain. In low-coral territories these preferred patches are likely scarce, prompting long patch residence times and high bite rates when they are located. Additionally, one confounding factor is the density of small benthic invertebrates consumed by these species. If there are fewer preferred benthic invertebrates in low-coral territories, then these two species may show differences in behaviour that reflect the abundance of their primary food rather than the corals themselves.

Three key mechanisms offer plausible explanations for the behavioural differences we have observed. First, these differences may reflect activational plasticity of foraging behaviour (Snell-Rood 2013), with individual butterflyfish adjusting their foraging behaviour to better suit a given territory (Sih et al. 2011, Tuomainen and Candolin 2011). The variation in behaviour we observed follow predictions of optimal patch usage (Krebs et al. 1974, Charnov 1976) or compensatory grazing behaviour (Penning 1986, Iason et al. 1999), which can be achieved through short-term behavioural adjustment (i.e., activational plasticity), adding support to this idea. However, without repeated sampling of individuals across multiple territories, plasticity cannot be confirmed directly. Secondly, it is possible that site-level differences in foraging behaviour between the bleached and unbleached reefs could be driven by evolutionary effects. Differences between sites could result from allopatric divergence in foraging behaviour (Palumbi 1994), rather than resulting directly from differences in habitat composition. Additionally, there could be other site-level habitat differences which are not captured by overall coral cover (ex. structural complexity, species assemblages), which might explain some of the site-level behavioural differences. However, alternate models focused on within-site variation (Table S4.1) confirm that both patch residence

times and bites per patch are well predicted by coral cover within sites. For both of these traits, model predictions along the gradient of coral cover were virtually identical to those that included between-site variability. Therefore, it appears that behavioural differences cannot be attributed to latent site-specific factors alone. Third, behavioural differences between low and high-coral territories could result from environmental filtering of behavioural types. Individuals within a given species may vary consistently in their foraging behaviour, having a specific behavioural type (personality/behavioural syndrome; Sih et al. 2004, Sih and Bell 2008). As a result of habitat filtering (Kraft et al. 2014), individuals are only able to settle in habitats where their behaviour is appropriate (e.g., Brodin et al. 2013, 2019). If, for example, low-coral territories are unsuitable for individuals with a more territorial behavioural type (high aggression, long patch-residence), then individuals of this type will be unable to settle in these zones, producing a trend in behaviour like that seen here. It is unclear which of these mechanisms is dominant in driving these variations in behaviour and the extent to which these factors could interact.

The effect of food disturbance on bite rate seen here follows predictions of compensatory feeding from optimal foraging theory but can also be understood through the lens of functional response relationships. It has long been understood that for grazing species, food intake rate increases with the density of food available (Holling 1965, Gross et al. 1993), typically estimated in terrestrial systems as sward height or leaf area index. In this framework, food intake rate is a product of the individual's daily foraging time, bite size, and bite rate (Allden and Whittaker 1970, Hodgson 1985). Numerous studies have attributed the increases in food intake with increased leaf area index / sward height to an increase in bite size (e.g., Gong et al. 1996, Lang and Black 2001). However, as larger bites take longer to process, these are also typically associated with a slower bite rate (Hodgson 1985). It is also important to consider how changes in biting may allow grazers to

compensate for limitations on their potential food intake. For example, grazers whose foraging time becomes limited may compensate for this by increasing their bite size (Iason et al. 1999) or bite rate (Chen et al. 2013). Whether considered as a product of a functional response to high food availability, or a compensatory reaction to low food availability, bite rates and food availability appear to clearly be inversely related.

Coral cover alone better predicted patch residence times than when combined with variation in coral cover. Following the marginal value theorem, the decision to exit a given patch reflects the potential net energy gain (or gain in another currency) from continuing to forage in the patch, compared to moving to and exploiting another patch (Charnov 1976). In this way framework, a forager will remain in the patch as long as the instantaneous net energy gain within the patch is greater than the average rate of net energy gain within the nearby environment. For example, among chickadees, residence times within a given patch type were longer when surrounded by low-quality habitat than when surrounded by high-quality habitat (Krebs et al. 1974). It can then be predicted that average patch residence time should reflect whether or not individuals frequently find themselves surrounded by viable food sources, a condition influenced by both the availability and patchiness of food resources within their habitat. It was expected that each might be uniquely informative, however this was based on the assumption that the two factors would vary independently. Instead, variation in coral cover was significantly collinear with coral cover. Foraging areas with higher average coral cover were patchier, containing both intact coral colonies, as well as dead colonies or those that have become overgrown with algae, whereas foraging areas with lower average coral cover more consistently contained dead or overgrown sections. While both food availability and food patchiness are likely important in shaping conditions for patch exit

(McNair 1982), collinearity between these variables here prevents us from determining which may be a better predictor for patch residency.

Contrary to predictions, average movement duration was unaffected by coral cover. Following the marginal value theorem (Charnov 1976, Stephens and Krebs 1986), there is an association between the travel time to a given patch and the rate-maximizing patch residence time within that patch. In other words, foragers must compensate for the energy spent on a longer movement bout by adjusting their feeding effort within the patch, once it is reached. Given the changes in average patch occupancy seen here, it was predicted that average movement duration might follow similar patterns. However, this relationship may not be reciprocal. An increase in average movement may result in an increase in average patch residence time, however the reverse may not necessarily be true. Additionally, as average movement duration here is a summation of several feeding and movement decisions within the same feeding area, these effects may be obscured.

Despite uncertainty in the causes of variation in behaviour, the differences we see here fit conceptually with a variety of behavioural changes observed in butterflyfish populations after coral bleaching. Weakened territoriality is a common theme for coral feeding butterflyfishes after coral bleaching, or within low-coral zones, particularly among specialists. For example, immediately following bleaching in the Seychelles, Samways (2005) observed a breakdown of feeding territories for *Chaetodon trifascialis* and *C. trifasciatus*, with fish instead displaying roaming behaviour like that seen in low-coral territories here. Likewise, butterflyfishes on Iriomote have also reduced their aggressive behaviour following bleaching-induced mortality (Keith et al. 2018), as this behaviour becomes economically unviable when coral is scarce. Similarly, compared to high coral exposed areas, in low coral back reef zones the specialist, *C. baronessa*, has shown larger, less-aggressively defended territories (Berumen and Pratchett 2006). No difference was

observed in territory size or aggression for *C. lunulatus.* Additionally, pair-forming behaviour has also been observed to decline in butterflyfishes following coral mortality (Thompson et al. 2019), either due to the costs of sociality when coral is limited, or due to disruption of pairs via mortality. A variety of studies have observed changes in butterflyfish diet after coral mortality (Pratchett et al. 2014, Keith et al. 2018, Zambre and Arthur 2018), which might stem from a weakening of dietary preferences across species (including both *C. trifascialis* and *C. lunulatus*; see **Chapter 3**). This body of work suggests that not only does the specialist, *C. trifascialis*, have a broader diet in low-coral conditions, individuals in these areas show unique foraging behaviour, incongruent with a specialist diet or territoriality.

Despite potential changes in foraging behaviour, however, coral-feeding butterflyfish populations consistently decline following coral mortality (Wilson et al. 2014). Population surveys on Iriomote have shown significant declines in overall butterflyfish abundance two years following coral bleaching (see **Chapter 3**). In general, the degree to which mortality is experienced after bleaching directly relates to the level of reliance on hard coral for a given species, with obligate corallivores experiencing some of the most substantial losses (Wilson et al. 2014). Even if species can maintain an equivalent volume of food intake in low-coral conditions, species may still face population declines because of the nutritional quality, or assimilation efficiency of non-preferred food sources. Efforts to quantify nutritional quality of coral genera have been limited in scope, evaluating either C:N ratio (Graham 2007) or percentage protein content (Masterman 2012), with differing results. Namely, C:N ratio estimates were highest (lowest food quality) for *Pocillopora*, whereas *Pocillopora* were the highest quality when considering relative protein content. Differential value among nutrient categories should come as little surprise, and in reality, these fish will need to balance prey items with a variety of nutrient densities to produce a healthy diet

(Simpson and Raubenheimer 1993, Simpson et al. 2004). However, in spite of mixed results regarding nutritional quality, one apparent trend is that butterflyfish species show diminished body condition when consuming non-preferred corals (Pratchett et al. 2004, Berumen et al. 2005). In other fish species, reduced body condition often leads to negative effects on growth or reproduction (Jones 1986, Kerrigan 1997), though this has not been directly tested for butterflyfishes (see Berumen and Pratchett 2008). It is also possible this loss of nutritious corals may serve as a driving force behind some of the behavioural changes seen in this population. For example, declines in aggressive behaviour seen on Iriomote may stem from a lack of energy to initiate these behaviours (Keith et al. 2018). It remains to be seen the extent to which observed differences in foraging behaviour (as well as other changes mentioned above) might benefit growth or reproduction in low-coral habitats, and this (as well as in-depth nutritional analyses) are an important avenue for future research.

The most notable differences in foraging traits across coral availability we observed were for the specialist, *Chaetodon trifascialis*. Specialist foragers generally operate within a narrow range of habitat conditions (Van Tienderen 1991, "Grinnellian Specialization" Devictor et al. 2010). Generalists on the other hand can succeed over a large range of conditions (*But see* Remold 2012). Due to these differences, specialist species are often at the greatest risk of extirpation from anthropogenic disturbance events (McKinney 1997, Kassen 2002, Devictor et al. 2008). Particularly among coral-feeding butterflyfishes, *C. trifascialis* are predicted to be most vulnerable to disturbance, due to their disproportionate consumption of tabular *Acropora* corals such as *Acropora hyacinthus* (Lawton and Pratchett 2012, Lawton et al. 2012). For example, among reef-dwelling gobies, all species suffer substantial population declines after coral mortality, with the greatest of these experienced by specialists (Munday 2004). In the case of corallivorous

butterflyfishes, the long patch residence times and territorial behaviour of the specialist, *C. trifascialis*, are expected to be adapted for high fitness within high-coral conditions, but the species may not be as successful in low-coral conditions, even if their behaviour differs in these environments. Despite having a wider diet in low-coral conditions (see **Chapter 3**), the overall bite rate of *C. trifascialis* in these areas was substantially lower. Though reliable predictions of their survival will rely on the energetics and nutritional value of alternate food sources, our findings provide early indication that the species could face substantial losses as a result of bleaching, supported by population estimates two years after bleaching (see **Chapter 3**). While the exact mechanism underlying these behavioural changes is unresolved, our results suggest that when preferred food sources are lost, specialist species alter multiple foraging traits, which could further mediate ecological changes at the population and community level. More broadly, specialist foragers might show strong buffering to habitat change by altering foraging behaviour in the short-term, whilst also being vulnerable to the largest population declines in the longer-term.

4.6 Contribution of Authors

RFS, SAK, and AHB video recorded foraging observations of butterflyfishes. RFS and NAJG developed primary research questions and planned analyses. RFS completed all analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

4.7 Chapter Acknowledgements

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5. Fine-scale foraging behaviour reveals differences in the functional roles of herbivorous reef fishes

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Robert F. Semmler[1†], Simon J. Brandl[2,3,4,5†], Sally A. Keith[1], David R. Bellwood[6,7]

[1]Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, UK

[2]Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1SG, Canada

[3]PSL Université Paris: EPHE-UPVD-CNRS, USR 3278 CRIOBE, Université de Perpignan, Perpignan, 66860, France

[4]Laboratoire d'Excellence "CORAIL," Perpignan, 66860, France

[5]CESAB–- FRB, 5 Rue de ''École de Médecine, Montpellier, 34000, France

[6]ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, 4811, Australia

[7]College of Science and Engineering, James Cook University, Townsville, Queensland, 4811, Australia

† - Indicates shared first-authorship

5.1 Abstract

Efforts to understand and protect ecosystem functioning have put considerable emphasis on classifying species according to the functions they perform. However, coarse classifications based on diet or feeding mode often oversimplify species' contributions to ecological processes. Behavioural variation among superficially similar species is easily missed but could indicate important differences in competitive interactions and the spatial scale at which species deliver their functions. To test the extent to which behaviour can vary within existing functional classifications, we investigate the diversity of foraging movements in three herbivorous coral reef fishes across two functional groups. We find significant variation in foraging movements and spatial scales of operation between species, both within and across existing functional groups. Specifically, we show that movements and space-use range from low frequency foraging bouts separated by short distances and tight turns across a small area, to high frequency, far-ranging forays separated by wide sweeping turns. Overall, we add to the burgeoning evidence that nuanced behavioural differences can underpin considerable complementarity within existing functional classifications, and that species assemblages may be considerably less redundant than previously thought.

Keywords: complementarity, coral reefs, foraging behaviour, functional traits, movement

5.2 Introduction

Understanding how, why and when different species contribute to essential ecosystem functions has gained increased focus in recent years, with the aim to both advance fundamental knowledge and improve management (Tilman et al. 1997, Díaz and Cabido 2001, Folke et al. 2004; Bellwood et al. 2019). For both fundamental and applied research, it is not only important to identify species that are key to the maintenance of essential functions, but also to establish the extent to which species are functionally similar (underpinning redundancy) or different (underpinning complementarity) (Lawton and Brown 1993, Frost 1995, Nyström 2006, Blüthgen and Klein 2011, Burkepile and Hay 2011, Brandl et al. 2019). Complementarity essentially describes niche partitioning in an Eltonian, functional context (Brandl et al. 2019; Bellwood et al. 2019). Substantial complementarity has been documented within superficially homogeneous groups of flying insect pollinators (Blüthgen and Klein 2011), grazing subtidal urchins (Brandt et al. 2012), savannah ungulates (Pringle et al. 2014), and small desert herbivores (Thibault et al. 2010). However, for practical purposes a delicate balance is necessary between the benefits of tractability and the risks of oversimplification. On the one hand, it is necessary to ensure tractability or utility of functional groups, which requires collapsing diverse species into groups of ecologically similar entities, e.g., trophic groups or guilds. On the other hand, groupings may oversimplify ecological dynamics, masking important differences between species within the same functional category and their contributions to ecological processes (Körner 1994).

Ecosystems with high inherent species richness, such as coral reefs and tropical rainforests are characterized by a complex mosaic of biological interactions, and a wide variety of available of microhabitats (Gentry 1982, Reaka-Kudla 1997, Graham and Nash 2013). This complexity has spurred the development of functional group classifications, on coral reefs in particular (Bellwood

et al. 2004; Nyström 2006; Darling et al. 2012). Nevertheless, species within these groups may differ in a number of ways that could impact the delivery of their functions. Thus, to ensure that functions are maintained as species assemblages change, we need to know the extent to which species within the same broad functional entity differ from one another. It is doubtful that there is 'true redundancy' within functional groups; rather there will be some degree of complementarity, dependent on the scale at which behaviour is assessed (Brandl and Bellwood 2014). Within functional entities, complementarity of functional delivery can be a result of fine-scale partitioning of resources, which can be based on species-specific differences in targeted resources, or temporal and spatial patterns in their exploitation (Wellborn and Cothran 2007, Fründ et al. 2013). Species foraging patterns are likely to reflect all of these elements, thus providing a window into the extent of functional complementarity among species.

Foraging movements are determined by economic decisions to optimize the food resource gained per unit of energy expended (MacArthur and Pianka 1966). Thus, while not the only factors affecting movement, foraging movements depend both on dietary preferences and the abundance and patchiness of the food resources targeted (Stephens and Krebs 1986). For example, to account for long travel times and their associated costs, patchy food resources require long patch residence times (Charnov 1976). Additionally, low-quality patches will be depleted quickly below an energy gain per unit effort that maintains optimum foraging (McNair 1982). As a result, species that focus their diets on patchy or lower quality food items may have shorter patch residence times and greater exploration times (Stephens and Krebs 1986). Because foraging movement decisions are made based on the density and location of food resources, even among closely related species, these types of small differences in dietary preference can favor different foraging strategies (Pyke 1984).

In addition to these factors, patch use may also be impacted by the threat of predator (Brown et al. 1992, Catano et al. 2015) or competitor species (Mitchell et al. 1990).

Variations in foraging strategy are the result of adaptive changes that facilitate coexistence among species competing for space and resources (Tilman 1982, Chesson 2000). However, different foraging strategies are also likely to affect the spatial extent over which species perform their role (Nash et al. 2013, Nash et al. 2016). Efforts to identify a forager's spatial scale of operation through home-range assessments are useful but feeding activity can be heterogenous and concentrated within certain areas of the animal's range (Welsh and Bellwood 2012, Streit et al. 2019). As a result, assessments of animals' foraging movements can benefit from various types of behavioural observations across multiple spatial and temporal scales.

Coral reef fishes can overlap heavily in their broad use of habitats and in their contributions to ecosystem functions (Mouillot et al. 2014). Conservation actions have been adopted on the basis of these strategies to manage coral reef ecosystems with a particular focus on the role of herbivorous fishes (Green and Bellwood 2009, Adam et al. 2015a + 2015b, Chung et al. 2019). Herbivory by coral reef fishes was originally divided into four broad functional categories based on foraging strategies: grazers, browsers, scrapers, and bioeroders (Bellwood et al. 2004, Nyström 2006, Green and Bellwood 2009). These categories cover a suite of functions that facilitate reef resilience to disturbance, and can prevent them from shifting to less desirable, alternate states dominated by algae (Hughes et al. 2007). However, species within these groups are far from homogenous in their niches (Brandl et al. 2019; Bellwood et al. 2019). For example, browser species can differ strongly in their preference for algal food resources (Rasher et al. 2013; Streit et al. 2015, Puk et al. 2016), while grazers separate into species targeting the tips of algae (e.g., croppers) and species targeting particulate matter within algal turfs (e.g., Brandl and Bellwood

2016; Tebbett et al. 2017). Similarly, scraping and bioeroding parrotfishes differ substantially in their ingestion and post-ingestion treatment of resources (Clements et al. 2016, Adam et al. 2018, Nicholson and Clements 2020), leading to various refinements of the initial categories over the years (Brandl & Bellwood 2016; Siqueira et al. 2019). However, these classifications still focus primarily on diet and resources acquisition method. Few consider spatial dimensions of resource use. While reef herbivores are known to vary in their specific microhabitat use (e.g., horizontal, vertical, underside) (Fox and Bellwood 2013, Brandl and Bellwood 2014, Adam et al. 2018, Puk et al. 2020), fine-scale foraging movements and spatial resource partitioning in coral reef fishes remains poorly understood (Streit et al. 2019). Yet it is at this scale that resource partitioning and complementarity may be most strongly expressed, with significant effects for reef functioning (Ruttenberg et al. 2019).

We investigate the degree to which differences in foraging behaviour can transcend boundaries set by traditional functional group classifications. Specifically, we assess the fine-scale foraging movements of three coral reef herbivores: two grazer/cropper species *(Siganus corallinus and Siganus vulpinus*) and one scraper (*Scarus schlegeli*). We ask: How does foraging behaviour and space-use vary between species? Specifically, (1) which traits (speed, turning angle etc.) define the differences between their foraging paths? (2) Do short-term hourly movement patterns (*in situ* behavioural observations) reflect longer-term daily patterns of space use (assessed via active acoustic telemetry)? (3) Are there substantial differences in the scale of operation among species, and does this affect the spatial extent over which these species perform their functional role?

5.3 Methods

Field sites were located on reefs at Lizard Island, a granitic mid-shelf island on the Great Barrier Reef. We studied three species: two rabbitfishes *Siganus vulpinus* and *Siganus corallinus* (Fig.

5.1), and one parrotfish *Scarus schlegeli*. The two rabbitfishes are categorized as cropping herbivores that take discrete bites from small algae or cyanobacteria (i.e., grazers) (Brandl and Bellwood 2016; Hoey et al. 2013) and occur almost exclusively in stable pairs (Brandl and Bellwood 2013; 2015). By contrast, *Scarus schlegeli* lives in small groups and is a scraping herbivore that ingests the entire epilithic algal matrix (i.e., scraper) (Clements et al. 2016).

Figure 5.1 Photo of two *Siganus corallinus* individuals (credit: Victor Huertas).

While the vast majority of grazing herbivores on reefs have limited home ranges and exhibit strong site fidelity at the reef scale, there is considerable variation in the movements among both rabbitfishes (Brandl & Bellwood 2013; Fox & Bellwood 2011) and parrotfishes (Welsh & Bellwood 2011, 2012). The three species in the present study were selected to permit a comparison between two species commonly considered to be functionally equivalent (the two cropping

rabbitfishes), while anchoring these observations within the broader classification of grazing herbivores by including a functionally-different species (the scraping parrotfish). Foraging path observations were performed on Big Vicki's Reef (5 hectares) from Feb 7th – Feb 11th 2014, while the acoustic tracking was performed on Watson's Reef (2 hectares) from Apr 25th – May 4th 2012. Both reefs are on the leeward side of the island and represent typical backreef sites with low wave energy and depths between two and five meters. The two reefs are separated by a distance of approximately 2 km and represent broadly similar lagoonal habitats dominated by corals and turf algae. We chose to perform the two parts of the study on different reefs for several reasons: 1) since acoustic tracking involves the capture and manipulation of fishes, which may modify the individual's reactions to observers in the water, we considered it safer to avoid the reef that fishes were tagged on; 2) Big Vicki's reef offered a more expansive and slightly deeper reef environment, thus allowing for higher replication without the risk of re-sampling the same individuals, while ensuring a minimal observer effect from the snorkeler in the water.

5.3.1 Focal foraging path observations

We quantified the fishes' foraging movements *in situ*. A single snorkeler (SJB), equipped with a handheld global positioning system (GPS) unit in a waterproof case, which was set to automatically record its position every five seconds, performed the observations. We opportunistically located an adult of one of the three target species and followed the fish for 30 to 45 minutes. We followed the fish as closely as possible (snorkeling offering one of the least disturbing methods of observation; Welsh and Bellwood 2011), recording different behaviours (i.e., swimming and feeding behaviour). For each behaviour, the observer recorded the exact time of the event (hh:mm:ss) using a digital wristwatch that was precisely synchronized with the GPS unit. All focal observations occurred between 08:00 – 17:00, a time window during which most

herbivorous fish species are actively foraging. We considered a foraging bout to be finished once the fish stopped biting the substratum and assumed a horizontal position characteristic of swimming activity (Nash et al. 2012). During all observations, we ensured positioning directly above the focal individual (which restricted our observations to areas with depths >2m to ensure fishes were undisturbed by the observer). After 30 to 45 minutes (or when the focal individual showed signs of behavioural modification due to being followed by the snorkeler or contact was lost due to depth or visibility), the observer abandoned the focal individual in search of an individual of one of the other two species. Once individuals in all three species were followed, the observer took a haphazard turn, swam for at least 100 meters, and searched for another individual in any of the three target species. To avoid duplication, we spread efforts across different sections of the reef and took notes on size and color patterns of the observed fish.

5.3.2 Acoustic telemetry

To obtain a more detailed assessment of space use in the two rabbitfish species, we used active acoustic telemetry on five adult individuals of *Siganus corallinus* (in three pairs; SC1 and SC2, SC4, SC5 and SC6) and three adult individuals of *Si. vulpinus* (in two pairs; SV2, SV3 and SV4). An additional individual was tagged in each species but disappeared shortly after release, probably due to predation (Khan et al. 2016). While the behaviour of paired individuals will not be wholly independent from their partner, separation of individuals or exclusive treatment of only one partner can result in changes of behavioural patterns. To tag the individuals, we caught pairs using barrier nets on Watson's Reef and transported them immediately to Lizard Island Research Station in large bins full of fresh seawater, ensuring pairs were maintained. At the station, we placed pairs in separate large (300l) flow-through seawater aquaria. In the evening of the day of capture, we anesthetized each fish in a saline solution of tricaine methanesulphonate (MS-222, 0.13 g l^{-1}) and

surgically implanted an acoustic transmitter (Vemco V9-6L) into the gut cavity (cf. Brandl and Bellwood 2013). After closing the incision with sutures and ensuring full recovery from anesthesia, we held fishes in their tanks overnight. We returned the fishes to the exact site of capture the next morning.

Fish were allowed 48 hours to recover, after which we started acoustically tracking each fish from a 3.1 m kayak using a calibrated directional hydrophone (VH110) and an acoustic receiver (VR100, both Vemco) (Fox and Bellwood 2011; Brandl and Bellwood 2013). Tracking continued from 30 min before dawn to 30 min after dusk 117ifferex. 06:30 – 18:00). We maneuvered the kayak to obtain maximum signal strength from the respective tag every 15 minutes, while the receiver recorded the kayak's GPS position. We tracked each fish for three non-consecutive days and verified the identity and normal behaviour of the tracked individual via a short *in situ* validation by a snorkeler each day (identifying the tagged fishes through the visible surgical incision; Brandl and Bellwood 2013).

5.3.3 Data analysis

We performed all data analyses in R (R Core Team, 2019). For the snorkeler-based observations, we matched timed GPS recordings with recorded times for each feeding event to quantify the path between successive feeding events for each. From these, we calculated six traits to characterize different aspects of foraging behaviour or space use: 1) 95% minimum convex polygon (MCP) of space used during the observation, 2) mean swimming speed, 3) mean turning displacement (higher displacement = sharper turns) between successive movement bearings, 4) overall tortuosity of the feeding path, 5) number of feeding events minute^{-1}, and 6) average distance between feeding events (inter-foray distance). We computed MCPs using the package *adehabitatHR* (Calenge 2006), and distances (using the Haversine method) and bearings between points, using the package

geosphere (Hijmans 2016). We calculated overall path tortuosity as the ratio of the straight-line distance between the start and end locations, and the total distance travelled by the fish (following Secor 1994, Fulton and Bellwood 2002). We tested for differences between the three species in each of these traits with Analyses of Variance (ANOVA). To ensure normality and homoscedasticity of variances, it was necessary to log transform the MCP values. After transformation, MCP values for *Si. vulpinus* became normally distributed (Shapiro-Wilk: 0.88, p = 0.12) and MCP variance among species was homogenous (Bartlett: 5.64, df = 2, p = 0.06).

Furthermore, we visualized inter- and intraspecific variation in these traits with a non-metric multidimensional scaling (MDS) ordination based on a Bray-Curtis dissimilarity matrix (Gauch 1973). We ran the ordination on a square root Wisconsin transformed matrix to ensure that differences in scale between trait values did not influence the analysis (Del Moral 1980). We used a Permutational Analysis of Variance (PERMANOVA) to test for significant differences in the overall foraging strategies of the three species and tested for homogeneous multivariate dispersion between species using PERMDISP. Lastly, we used the SIMPER analysis to determine which traits contributed most to differences in foraging behaviour between species. PERMANOVA, PERMDISP and SIMPER tests were run on the transformed dissimilarity matrix using the package *vegan* (Oksanen et al. 2016).

For the active tracking data, we used the GPS points from each 15-minute intercept (choosing the highest-strength signal around the 15-minute mark) to compute kernel utilization distributions (KUDs) for each individual, which we used to estimate 95% daily foraging areas and 50% core areas for each individual (Brandl and Bellwood 2013). We calculated KUDs for each day and the cumulative GPS points across all days. We again used the package *adehabitatHR* (Calenge 2006).

We tested differences in cumulative daily foraging areas and core areas between the two rabbitfishes with two-sample t-tests.

Lastly, we also computed overall feeding rates (bites/min) and movement rates (meters/min) for each fish observed on snorkel. Specifically, our rationale was that differences in foraging strategy between species may be underpinned by fine-scale dietary differences. Differences in feeding efficiency between species may help to highlight this, as diets may provide more or less energy per bite. Feeding rates were calculated based on the total time spent feeding within each observation (with each feeding event estimated as five seconds), multiplied by previously established bite rates during feeding events, for each species (Brandl and Bellwood 2014). Feeding efficiency was calculated by dividing each individual's feeding rate by its movement rate. As with the six traits above, for these three factors we tested differences between species with ANOVA.

5.4 Results

Overall, we followed 29 individual fishes (counts: *Siganus corallinus* = 9 individuals; *Si. vulpinus* = 10 individuals; *Scarus schlegeli* = 10 individuals). Overall observation time totaled 17.4 hours (mean observation times: *Siganus corallinus* = 35.9 min ± 2.21 SE; *Si. vulpinus* = 34.5 min ± 2.54; *Scarus schlegeli* = 37.4 min ± 1.82) during which we recorded 1,190 feeding events. Foraging patterns differed for the three fish species, both within and across functional group boundaries. Variation in short-term foraging movements (Fig. 5.2) was mirrored by daily space use in the two rabbitfishes, where both 95% daily foraging areas and 50% core areas of *Si. vulpinus* were significantly larger than those of *Si. corallinus* ($t(6) = -6.00$, $p < 0.001$, and $t(6) = -6.28$, $p < 0.001$, respectively (Fig. 5.3). Overall, we found significant variation between species for five of the six

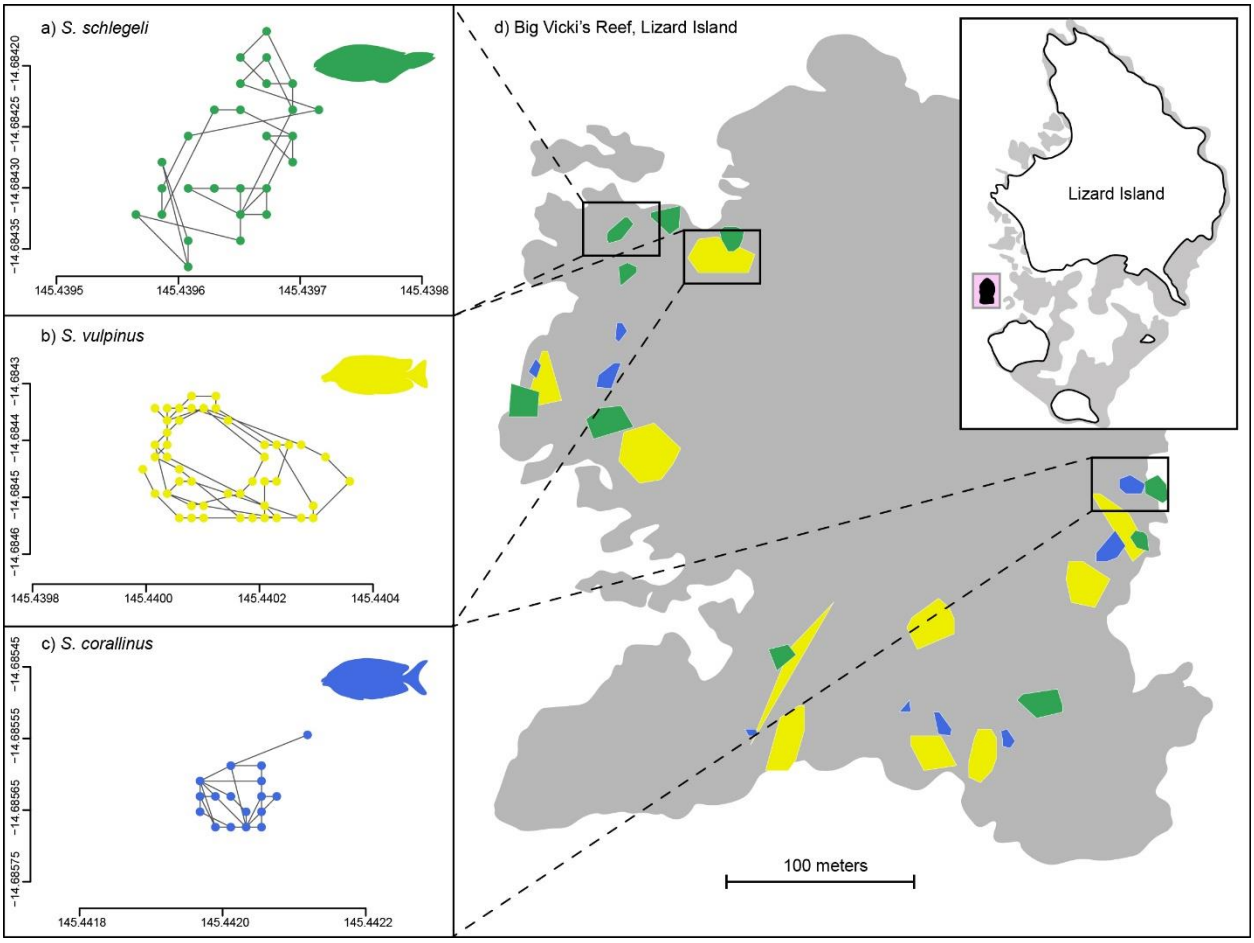

Figure 5.2 Foraging paths and resulting size and distribution of short-term feeding areas (direct observation). A-C) Example foraging paths for all three species. Green = the parrotfish *Sc. schlegeli*, yellow and blue = the rabbitfishes, *Si. vulpinus* and *Si. corallinus*, respectively. Dots represent foraging locations, while lines represent vectors between foraging events. Path insets not scaled by area, but relative size can be seen in the wider figure. D) Distribution of feeding areas (MCP) for each species on Big Vicki's Reef with inset showing location of Big Vicki's Reef on Lizard Island, colors as above.

movement traits we investigated (Fig. 5.4). Specifically, there were significant differences in the log of foraging area covered ($F_{2,26} = 21.96$, $p > 0.001$), mean speed of travel ($F_{2,26} = 3.98$, $p = 0.031$), mean turn angle ($F_{2,26} = 4.71$, $p = 0.018$), feeding frequency ($F_{2,26} = 9.44$, $p > 0.001$), and meaninter-foray distance ($F_{2,26} = 7.41$, $p = 0.003$). *Si. corallinus* had the smallest mean foraging area, while *Si. vulpinus* had the largest. We found a similar relationship for mean speed, with *Si.*

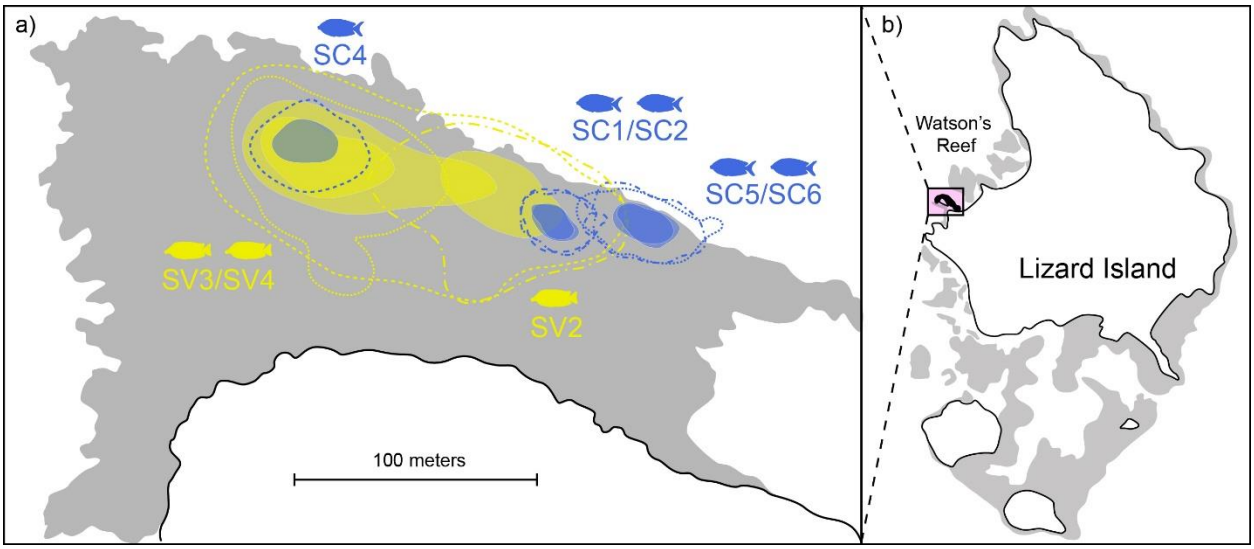

Figure 5.3 Relative size of daily foraging areas (acoustic telemetry). (A) Spatial distribution of daily foraging areas on Watson's Reef. Dotted and dashed lines mark the 95% Kernel Utilization Distributions (KUDs), while filled, transparent areas mark the 50% core areas. Fish numbers are given for all paired and the two singular individuals. Colors as above. (B) Location of Watson's Reef on Lizard Island.

vulpinus travelling at greater speeds than *Si. corallinus*. *Si. vulpinus* also took wider turns between feeding bouts compared to *Si. corallinus* and *Sc. schlegeli* (Fig. 5.4). However, despite difference in turning angles, we found no significant differences for the overall tortuosity of foraging paths. While mean tortuosity did not differ, variance in path tortuosity was substantially larger for the rabbitfishes than for *Sc. schlegeli*. *Sc. schlegeli* had more frequent foraging bouts than *Si. corallinus*, and *Si. vulpinus* had longer inter-foray distances than either of the other species. As would be expected from the results above, species identity was significant in determining foraging behaviour, explaining 42% of variance among individuals ($R^2 = 0.42$, $p < 0.001$, Fig. 5.5).

All species showed similar levels of intraspecific variability in foraging traits; multivariate dispersions were not significantly different between species ($p = 0.060$). Despite not differing significantly in the univariate analysis, path tortuosity contributed to differences between species

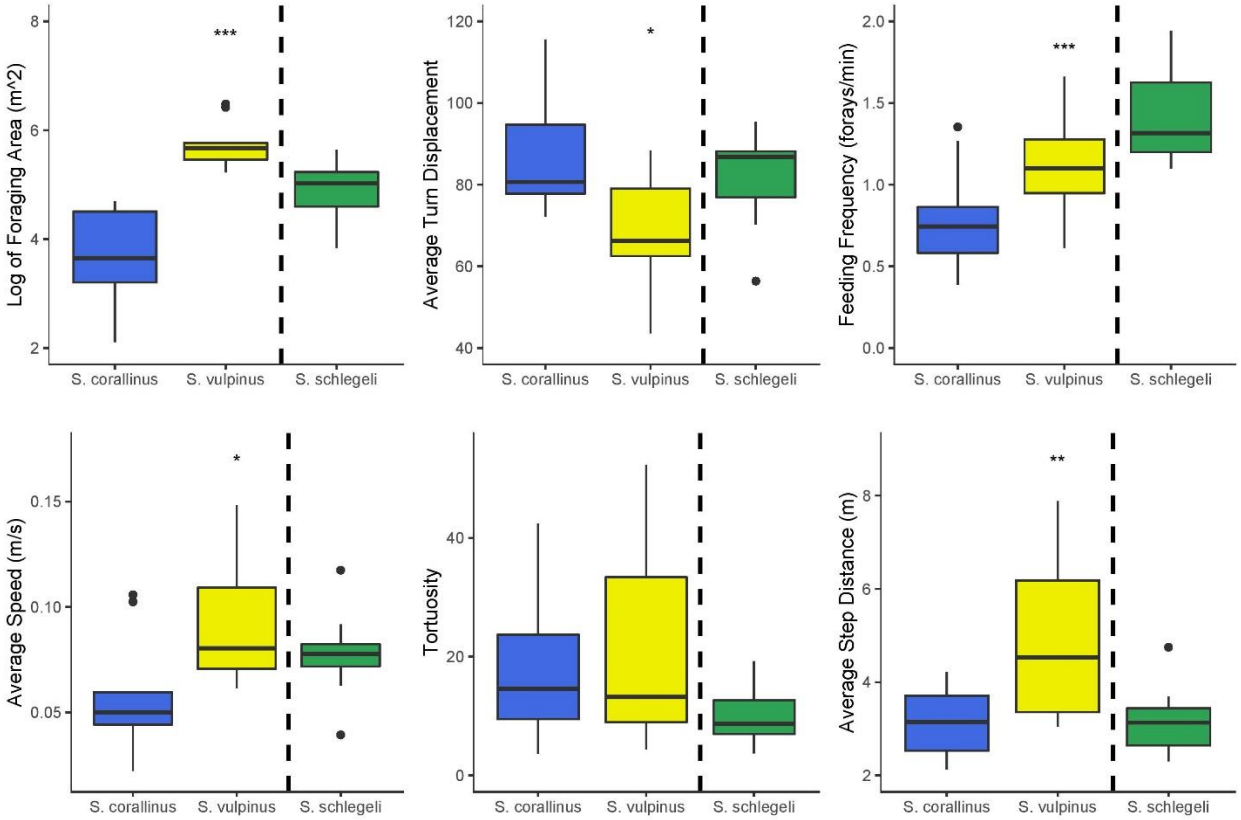

Figure 5.4 Differences in the six metrics used to evaluate foraging paths of the three species. Asterisks indicate significant differences among species via ANOVA. *Si. vulpinus* foraging movements are characterized by: large areas, wide turns, higher speeds, and longer inter-foray distances; *Si. corallinus* foraging movements are characterized by: small areas, sharp turns, low feeding frequency, low speed, and short inter-foray distances; *Sc. schlegeli* occupy intermediate positions but display the highest frequency of foraging. Boxplots represent the median and interquartile range of each foraging trait. Dashed lines separate the two grazing rabbitfishes from the scraping parrotfish

within the multivariate analysis. Differences between species were most strongly predicted by the size of their foraging areas, the tortuosity of their foraging paths and the mean turning angle between feeding events, with each of these traits explaining over 20% of the difference between any two species. Mean speed was the least informative trait, explaining < 10% of the average difference between any two species. Differences between the parrotfish *Sc. schlegeli* and the rabbitfish *Si. corallinus*, were mostly driven by a tighter (18%), smaller (19%) and more tortuous

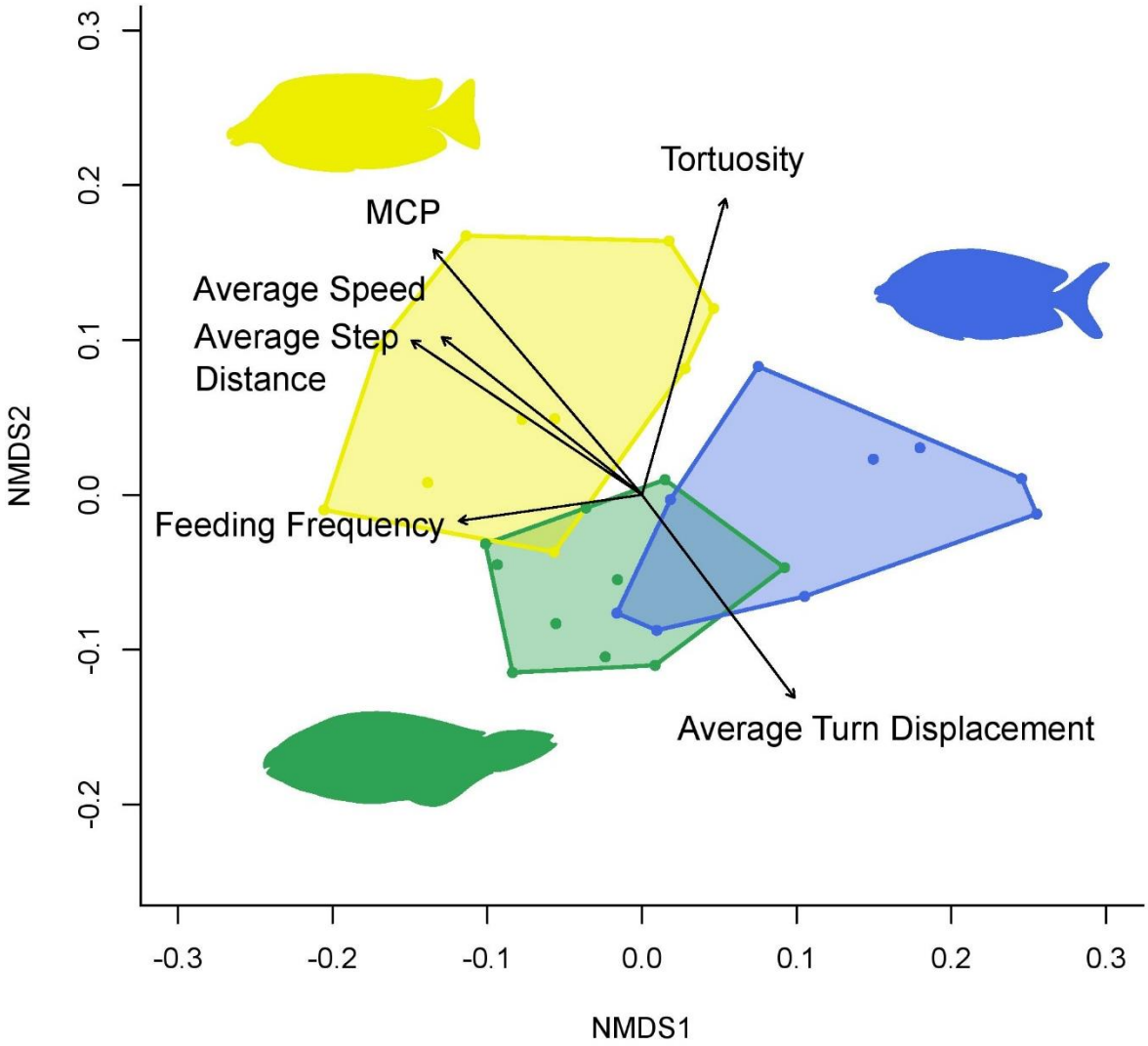

Figure 5.5 Non-metric multidimensional scaling ordination depicting differences in foraging paths of three species: the rabbitfishes *Siganus vulpinus* (yellow), *Si. corallinus* (blue), and the parrotfish *Scarus schlegeli* (green). Convex hulls represent minimum convex polygons for all individuals of a species. Vectors represent the loadings.

feeding path (24%) for the rabbitfish. Similar differences were reflected between the two rabbitfish, with large proportions of variance defined by tighter turns (26%), and a smaller feeding area (29%) for *Si. corallinus*, however a less tortuous path (20%) than *Si. vulpinus*. Differences between *Sc. schlegeli* and *Si. vulpinus* were also most strongly determined by a larger (19%) more

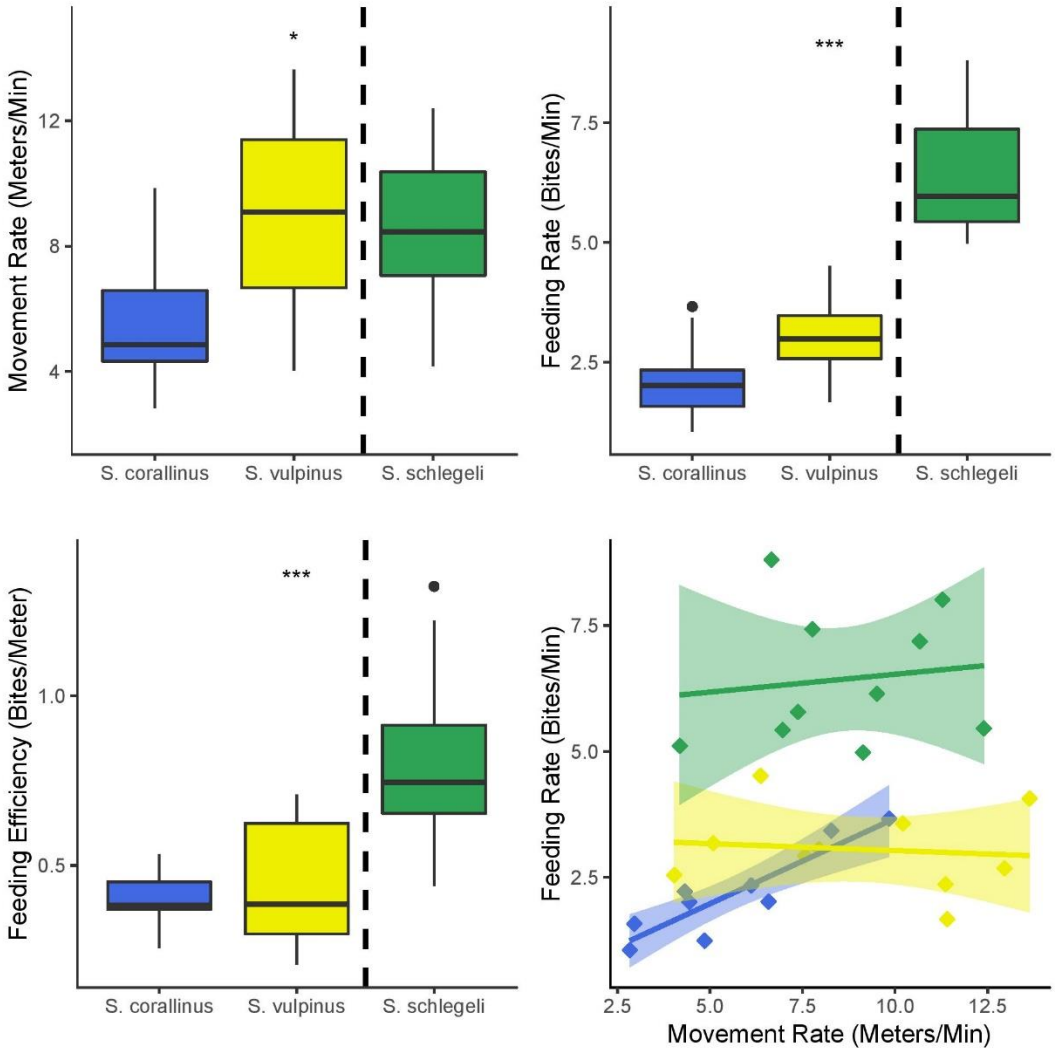

Figure 5.6 Feeding Rate, Movement Rate, and Feeding Efficiency of the three species. Asterisks indicate significant differences among species via ANOVA. Boxplots represent the median and interquartile range of each foraging trait. Dashed lines separate the two grazing rabbitfishes from the scraping parrotfish.

tortuous feeding path (21%) for the rabbitfish, as well as a faster feeding frequency (21%) for the parrotfish.

Lastly, species differed significantly in their feeding rates ($F_{2,26} = 44.55$, $p > 0.001$), movement rates ($F_{2,26} = 4.33$, $p = 0.024$), and their resulting feeding efficiency ($F_{2,26} = 12.71$, $p > 0.001$) (Fig. 5.6). *Si. corallinus* had the lowest movement rates, with both *Si. vulpinus* and *Sc. schlegeli* moving

faster. Based on unique foraging events and bite rates, the parrotfish took many more bites per minute than either rabbitfish species. Due to these differences, the feeding efficiency of the parrotfish was higher than either rabbitfish. While across the three species, a positive relationship between movement and bite rates was visible, only *Si. corallinus* showed an intraspecific trend where individuals traveling farther took more bites per unit time.

5.5 Discussion

Categorization of species based on their functional roles is a useful concept in ecology and conservation. However, behavioural differences among species within the same group may result in functional variation that is unaccounted for in broad categories. Our results demonstrate behaviourally-mediated diversity in functional roles of herbivorous fishes within and across functional groups, resulting in complementarity in their niches and spatial differences in the delivery of their functional roles. The differences in fine-scale foraging paths of the grazers, *Si. corallinus* and *Si. vulpinus*, are reflected in their broad-scale, reef-scape movements. Both fine-scale activities and sustained broad-scale movements are critical components of animals' energy budgets, but they also shape their functional roles within ecosystems, especially in a spatial context.

In our analysis, we found clear differences in foraging behaviour between the three fish species, even those within the same functional group and genus, i.e., grazing rabbitfish. Feeding frequency was the primary trait that differentiated the two functional groups, both in terms of the number of forays per minute and the number of bites per minute. This difference could be expected as scrapers primarily remove epithelial algal matrix from flat or convex surfaces, which can be more readily located without disrupting movement (Brandl and Bellwood 2014, Clements et al. 2016). The two

grazers, on the other hand, will inspect holes or crevices for patches of algae to crop (Fox and Bellwood 2013; Brandl and Bellwood 2015), leading to slower bite rates and less frequent feeding events. As a result of its fast feeding rate and intermediate movement rate, the parrotfish appears to be the most efficient, or least selective, forager, taking the largest number of bites while traveling only short distances between those bites.

As well as the expected behavioural differences between functional groups (i.e., grazers vs. scrapers), there were substantial differences between the two grazers. *Si. corallinus* moved slowly, focusing feeding effort within a very small area of the reef, and took sharp turns to stay within this core area. In contrast, *Si. vulpinus* ranged widely over a considerably larger feeding territory and travelled substantial distances between forays in a roughly circular, and remarkably predictable pattern. Though sample sizes for acoustic tracking were limited and included non-independent paired individuals, we have considerable confidence that these differences were reflected in the daily foraging areas of each species as well, with *Si. corallinus* occupying a much smaller foraging area than *Si. vulpinus*. Complementary scales of space use among these two species indicate that both species will contribute more strongly to algal grazing than either could alone, which holds important implications for the management of herbivory on coral reefs (Topor et al. 2019).

Some of the differences in the foraging search patterns of the rabbitfish species could be driven by differences in their diets. While both are considered grazers, *Si. corallinus* primarily targets small, dense red algae, while *Si. vulpinus* mostly consumes cyanobacteria (Hoey et al. 2013). Furthermore, *Si. vulpinus*, with its extremely elongated snout, appears to obtain most of its food from deep crevices and interstitial microhabitats compared to *Si. corallinus*, which targets shallower crevices that it can exploit with its more moderate head morphology (Brandl and Bellwood 2014, 2016). Differences in foraging behaviour between the two species may be driven

by the spatial organization of these resources on reefs and their patchiness; while small red algae and shallow crevices can be expected to occur frequently throughout the reef matrix, deeper crevices with dense mats of cyanobacterial growth are less common (Brandl et al. 2015, Harris et al. 2015). These differences closely resemble those recorded in a range of wrasse species on coral reefs (Fulton and Bellwood 2002). Additionally, cases of food distribution affecting foraging strategies, like those seen here, have been seen in a variety of systems, including ant colonies (Lanan 2014). However, we currently lack detailed information on the spatial organization of algal resources needed to determine the exact relationships between resource distributions and the fishes' foraging movements. Differences in foraging paths may be influenced by many aspects of the targeted food resources, including their patchiness, within patch density, or their nutritional and energetic quality (Schatz and McCauley 2007).

While both red algae and cyanobacteria are thought to be nutritionally poor, cyanobacteria appear physically less dense than corticated red algae, lacking the same hard external tissues. A lack of hard tissues could make cyanobacteria easier to mechanically process when feeding, consistent with observations of larger handling times for crustacean prey (Hoyle and Keast 1987). Under the patch model of optimal foraging theory, a foraging strategy involving long travel to distant patches is linked with low quality of nearby patches (Charnov 1976). A forager will leave a patch and continue searching when the rate of energy gain in a patch has been reduced below what could be obtained elsewhere (Stephens and Krebs 1986). If cyanobacteria are particularly easy to process, then the "quality" (here related directly to quantity) of cyanobacteria patches may be reduced sooner than that of red algae, prompting patch exit and further exploration. These differences could result in a foraging strategy with shorter patch residence times, and larger territory sizes on average

(Charnov 1976, Stephens and Krebs 1986). Corticated algae patches on the other hand may maintain their quality long enough to favor long patch occupancy, and smaller range sizes.

Another difference between these two food sources is that cyanobacteria are considered unpalatable for many species and produce metabolites to deter their consumption (Paul et al. 1990, 1992; Capper et al. 2006). Toxin constraint models predict foragers should exhibit partial food preferences, consuming multiple food types even when a toxin-producing food item is most nutritionally profitable (Stephens and Krebs 1986). In this way profitability of food items will be balanced against toxins they contain. This balance was illustrated for reef herbivores in a study by Hay et al. (1994) where, when given a choice between a control food source and one supplemented with metabolites, reef and seagrass parrotfishes almost exclusively consumed the control food sources. Because of this, *Si. vulpinus* may need to supplement its diet with other food sources that, while less preferred, produce less toxin. For instance, dense, mat-forming species of cyanobacteria (e.g. genus *Lyngbya)* are expected to produce more toxins than their sparser counterparts (Cissel et al. 2019). Consequently, short patch residence times and wide movements for *Si. vulpinus* may be due to the quicker depletion of less-dense cyanobacteria patches that produce less toxin. However, without similar choice experiments on these species, it is unclear how much rabbitfishes are constrained by cyanobacterial metabolites.

The feeding efficiency approach given here reveals some intriguing differences between species. However, without clear information on nutritional content and assimilation efficiency these comparisons are solely exploratory. Energy budgets are complex and, in addition to these nutritional factors, are a result of other properties like body size and swimming style/speed. The two families differ substantially in their locomotion: while rabbitfishes rely largely on undulating caudal and pectoral-caudal propulsion, wrasses (such as parrotfishes) almost exclusively use

flapping pectoral propulsion (Fulton 2007). Energetic studies have suggested that flapping, pectoral propulsion (labriform swimming) is more energy efficient than undulating (Korsmeyer et al. 2002) or rowing pectoral propulsion, the latter of which rabbitfishes frequently employ for fine-scale maneuvering (Jones et al. 2007). Thus, in principle, one may expect that the parrotfish could meet energetic demands with lower feeding efficiency than the two rabbitfish species. Nevertheless, there are important other considerations that can underpin energetic demands, such as energy and nutrient content of food items. First, given the strong relationship between body mass and metabolism, a *Sc. schlegeli* of 20cm (192 g, estimated using length-weight relationships) would have a resting metabolism approximately nearly 50% higher than than a *Si. corallinus* of equal length (117 g) and would require substantially more energy (Clarke and Johnston 1999). Second, by scraping microbes from the calcareous reef matrix and winnowing through unwanted material, energetic and nutritional net gains per bite may be low for the parrotfish (Clements et al. 2016), thus necessitating high ration of bites per unit distance covered during foraging despite the lower energetic demands of labriform locomotion. In contrast, procurement of algae may be relatively easy for the two rabbitfishes. Our findings highlight the important need to investigate reef herbivores through an energetic and nutritional lens to fully understand the drivers and consequences of their foraging patterns.

Protecting valuable ecosystem functions requires an understanding of variations within and between functional entities (Brandl et al. 2019). Our work highlights the importance of foraging behaviour as an important dimension in species management, as nuanced behavioural differences among fish species can indicate strong species-specific patterns of space and resource use that can result in complementarity in functional roles. This complementarity is ultimately driven by

differences in species' energy budgets, which emphasizes the need for detailed examinations of consumer species, their food choices, and the functional consequences of this interaction.

5.6 Contribution of Authors

RFS extracted relevant foraging traits from GPS data, developed the primary research questions along with SJB, performed all data analyses, and wrote the first draft of the manuscript. SJB performed all focal observations and managed acoustic tracking efforts. All authors contributed substantially to revisions.

5.7 Chapter Acknowledgments

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6. General Discussion

6.1 Key Findings

In this thesis I have focused on the value of understanding changes and variations in foraging behaviour, both within and between species. My work evaluated potential behavioural responses to human-induced rapid environmental change (Sih et al. 2011, Tuomainen and Candolin 2011), specifically bottom-up effects of altered food availability (Wong and Candolin 2015, Wilson et al. 2020). Using coral reef mortality and corallivorous fish as a model system, I evaluated species-level and community-level outcomes for changes in two important aspects of corallivore behaviour: dietary specialization and patch use. These efforts highlighted the importance of understanding change and diversity in foraging behaviour among species. I then applied a similar framework to a species group critically important to coral reef management. I investigated interspecific variation in the foraging behaviour of coral herbivores, as well as possible dietary and physiological explanations for these differences, and their potential conservation implications.

In **Chapter 2**, I reviewed the extent to which bottom-up effects have been seen to alter three important aspects of foraging behaviour: home range size, feeding distances, and aggression. I found taxonomic biases in the resulting research, with most studies focused on either mammals or birds. These make sense given existing biases toward these groups in conservation and behaviour research overall (Bonnet et al. 2002, Clark and May 2002, Rosenthal et al. 2017). As predicted from optimal foraging relationships (Ford 1983, Covich 1976), studies on territory size and feeding distance frequently observed a negative relationship with food availability, however this was not a significant effect for home range size. Additionally, studies on aggressive behaviour were split evenly between negative and positive relationships with food availability, as predicted (Enquist

and Leimar 1987, Peiman and Robinson 2010). The strict data requirements of the study led to a limited number of datasets (n= 43) that could be included in the meta-analysis. However, there was some indication of context-specific factors that may have a weak moderating effect on the strength of a space-use response. The two factors that were seen to have the largest effect on the strength of the response were predator taxonomy (mammals were more likely to show an increase in space-use under lower food availability) and prey seasonality (predators with seasonally fluctuating food sources were less likely to show an increase in space-use under lower food availability). Notably, the stronger responses for mammals are a particular concern when generalizing predictions from optimal foraging theory to less frequently studied groups. To reasonably predict changes in forager behaviour for management purposes, a deeper understanding of these constraints is needed.

In **Chapter 3**, I evaluated how reduced food availability (bleaching-induced coral mortality) affects dietary specialization, and how resulting dietary changes affect the structure of coral-corallivore networks. Consistent with predictions of the optimal diet model (Emlen 1966), I found that after coral mortality, coral-feeding fish had broader and more even diets. Moreover, these changes in diet appeared to be driven by a weakening of dietary preferences, rather than resulting from prey-switching (Murdoch 1969, Cornell 1976). This response led to a reduction of resource overlap at the genus-level, as many corallivores had specialized on *Acropora* corals prior to bleaching and these were most strongly affected by the bleaching event (Marshall and Baird 2000, Loya et al. 2001). Dietary changes led to substantial change in the coral-corallivore network, with a majority of this change due to rewiring of interactions. These changes in network structure continued in the second year following the coral bleaching event. After bleaching, the overall

interaction network was more connected, less specialized, and interactions were spread more evenly among species.

In **Chapter 4**, I investigated the degree to which butterflyfish foraging behaviour varies between low and high-coral environments, whether this differs substantially between species (particularly between specialists and generalists), and whether differences in foraging behaviour follow predictions from optimal foraging theory. I found that there are significant differences in foraging traits, with some of these shared among species, and others unique to individual species. For example, all species increased their instantaneous bite rates in low-coral areas in line with expectations from compensatory grazing behaviour in terrestrial herbivores (Chen et al. 2013). However, the most notable difference was that the specialist, *C. trifascialis*, has much shorter patch residence times within low-coral territories, a sharp difference from its strong territorial behaviour under normal conditions. In spite of altered behaviour in the specialist, it maintained a significantly lower overall bite rate in low-coral territories, which, in combination from expected lower nutritional quality of alternate prey (Pratchett et al. 2004, Berumen et al. 2005), could explain rapid population declines for these species after disturbance (Wilson et al 2014).

In **Chapter 5**, I applied a similar framework to a species group critical to coral reef management. I evaluated the extent to which foraging movement behaviour varies within and between different functional groupings of coral reef herbivore species, whether differences in short-term movements reflect overall differences in daily space-use, as well as any potential dietary or physiological explanations for these differences in behaviour. Among the three herbivore species evaluated there was substantial variation in movement behaviour both within and across species, with intergroup differences (between grazer and scrapers) primarily defined by differences in movement speed and feeding frequency, and with intragroup differences (among grazers) primarily defined by turn

angle and territory size. These differences may stem partially from the differential distribution, processing efficiency, or nutritional quality / palatability of their preferred food sources. Particularly, the differences in movement behaviour among grazer species highlights potential complementarity in the scale of their functional delivery and together these species may contribute more strongly to grazing than either could alone.

6.2 Synthesis

6.2.1 Interplay between optimal foraging responses

Chapter 2 illustrates several potential constraints on optimal foraging responses, however another possible source of context-specific outcomes not explored in this systematic review is better highlighted by the interplay between the results of **Chapter 3** and **Chapter 4**. After food loss, butterflyfish species appear to change their dietary specialization in a similar fashion, but the same is not true for their patch usage. This highlights the potential for change in one aspect of foraging behaviour to prevent, or alter, change in another aspects. The reasons for this may stem from how optimal foraging models are structured.

Optimal foraging models have evolved in a variety of ways over the years since their inception, tackling issues such as incomplete information / learning (Stephens 1987, Dall et al. 2005, Dunlap and Stephens 2012), variable handling times (Sih 1980, Anderson 1984), and multiple currencies (Simpson and Raubenheimer 1993, Simpson et al. 2004). However, the initial versions of these models as used here made a number of assumptions that can lead to issues when multiple aspects of foraging behaviour change. Emlen's optimal diet model predicts a diet based on the energetic benefit of an item's inclusion, taking into account its handling time and abundance within the environment (Emlen 1966, Charnov 1976a). To keep calculations simple, this model assumes a

set handling time for each food type, and doesn't account for how changes in foraging behaviour might affect the ease with which food items are obtained and processed. Similarly, in its initial form, the marginal value theorem predicts optimal patch usage based on the gain of energy within a given patch, relative to the average potential energy gain across the environment (Charnov 1976b). It assumes a set gain function for a given forager within a patch, and doesn't account for how changes in diet might affect the relative gain of different patches. If these factors are not directly accounted for, the predictive quality of either of these models is subject to the degree of interplay between changes in diet and foraging behaviour.

Results of **Chapter 4** provide a couple of interesting patterns that may be likely to play out when both diet and foraging behaviours are predicted to change. These patterns may tie in closely with a given species' initial level of dietary specialization. In some cases, changes in both diet and foraging behaviour could occur independently from one another, with a change in one having no bearing on the ability or likelihood of changing another. This may be especially true for generalists, for which, because of their already diverse diets, further dietary expansion should have little influence on whether changes in patch usage are beneficial. On the other hand, for a specialist such as *Chaetodon trifascialis*, the behavioural changes predicted from optimal foraging theory (increased patch residence time) may not prove as beneficial if the species is also experiencing a notable dietary expansion. As a result, we instead see a shift in patch use behaviour in the opposite direction, with patch usage in low-coral areas more similar to that of the generalists. If the diet of *C. trifascialis* had remained specialized on tabular *Acropora* corals in low-coral conditions, then the predicted changes in patch usage behaviour may have been observed.

Moreover, another difficulty in applying these models is the assumption that all prey of a given type provide equal nutrition (Emlen 1966, Charnov 1976a). In reality, food items of the same

species can vary substantially in size (Werner and Hall 1974, Turner 1982) and quality (Chapman et al. 2003, Mitra and Flynn 2005). It is for this reason that many tests of the optimal diet model treat prey of different size classes as separate diet entities (e.g. Werner and Mittelbach 1981), as predators may have clear patterns of size selection. However, nutritional quality is less easily determined visually. In the case of corals, while there are some trends in nutritional quality among taxa (Graham 2007, Masterman 2012), corals may also vary in nutritional quality from colony to colony, particularly as a result of bleaching and subsequent coral health (Grottoli et al. 2004). For example, mucus-feeding corallivores often seek out recently bleached tissue (Cole et al. 2009), as thermal stress induces corals to produce more nutritious mucus (Wright et al. 2019). However, in general corallivores avoid bleached colonies after this initial increase, as bleached colonies can often be depleted of nutritious lipid reserves (Grottoli et al. 2004). As a result of bleaching, corals will often use-up stored lipids to compensate for losses in photosynthetic capability (Fitt et al. 1993). A complete understanding of dietary selection will have to account for changes in the nutritional quality of corals as a food source.

6.2.2 The functional importance of altered corallivory

Chapter 5 considers the foraging behaviour of reef herbivores from a functional perspective, showing the importance of variation or change in reef fish behaviour, and how this may impact management**. Chapter 3** and **Chapter 4** on the other hand, primarily focused on the effects of altered corallivory on the corallivores themselves. However, it will be equally important to evaluate corallivory from a functional perspective and consider the effects of altered corallivory on corals and their survival after bleaching. Butterflyfish grazing of coral tissues is generally thought to be less harmful to corals than consumption by scrapers and bioeroders, because butterflyfish typically remove individual coral polyps, with minimal damage to the coral skeleton

(McClanahan et al. 2005, Rotjan and Lewis 2008). Nonetheless, changes in butterflyfish diet and foraging behaviour may raise important concerns regarding the recalcification of corals following disturbance, the spread of coral disease, and the reuptake of coral symbionts.

While physical damage from butterflyfish corallivory is minimal compared to other taxa, the combined effect of tissue removal across butterflyfish populations can add up. Recent estimates project that butterflyfish corallivory can remove an average of 9-14% of a reef's live tissue biomass annually, and this undoubtedly places some energetic strain on colonies (Cole et al. 2011). **Chapter 3** further evidenced how butterflyfish corallivory is directed primarily onto *Acropora* species and this is reflected in consumption estimates, with the annual consumption of tabular *Acropora* reflecting 52-79% of those species' annual energy production (Cole et al. 2012). *Acropora* corals are among the fastest growing corals, with high linear extension rates (Pratchett et al. 2015). However, after bleaching-induced mortality of Acropora colonies, these feeding efforts are then redirected onto other genera such as *Montipora* and *Pocillopora*. It is unclear how shifting of butterflyfish corallivory onto slower growing species may affect their health and survival in the long term and this is an important avenue for future research.

Work has shown that, in several cases, corallivore species may contribute to the spread of coral disease (Rice et al. 2019). Specifically, with regard to butterflyfishes, these results are mixed. Some butterflyfishes may preferentially seek out diseased tissue (Chong-Seng et al. 2011, Noonan and Childress 2020), and overall butterflyfish abundance is positively correlated with disease presence (Raymundo et al. 2009). Simultaneously, aquarium studies of direct spread have shown *Chaetodon capistratus* can accelerate the spread of disease (Aeby and Santavy 2006), whereas *Chaetodon plebeius* feeding might not damage coral tissues enough to sufficiently promote infection (Nicolet et al. 2018). Nonetheless, careful consideration must be given to any potential

role butterflyfishes can play in disease spread or management. Just as increases in dietary breadth form new connections within interaction networks, it is possible these connections may also serve as a vector for disease transmission among colonies that were previously isolated from one another. Moreover, it is possible that if feeding by butterflyfishes cannot cause direct infection, then consumption of diseased tissue by butterflyfishes could actually slow the spread of disease (Chong-Seng et al. 2011). Additional efforts are needed to identify the exact role butterflyfish corallivory plays in disease spread, and how changes in dietary specialization may affect these functional impacts.

In spite of these potential risks, corallivory may contribute important functional benefits to reef recovery as well. Recent work has shown that corallivory may serve an important role in the transfer of coral symbionts, as corallivore feces can serve as reservoirs for live symbionts (Castro-Sanguino and Sánchez 2012). In particular, some of the strongest impacts may delivered by obligate corallivore species, with their waste containing live cell concentrations five to seven orders of magnitude higher than in the surrounding sediment or water (Grupstra et al. 2021). Just as new connections between coral and corallivore may serve as sources of potential infection, so may they help coral species access symbiont reservoirs. This means that while continued corallivory by butterflyfishes poses potential risks to corals through consumption or disease, the continued presence of these fishes may also be critical in ensuring that bleached colonies can reuptake algal symbionts and recover from bleaching. Further efforts must be taken to understand the functional importance of corallivory, both in light of this new information, as well as considering how broadened corallivore diets may modulate their positive and negative effects on the coral community. In particular, a broad understanding of the functional traits and contributions within and across corallivore species (*sensu* Mouillot et al. 2014), is a valuable research need.

6.3 Future Research

This work opens up a variety of new avenues for future research. Specifically, this thesis highlights a need to better understand the nutritional benefit of corallivory, changes within coral reef interaction networks, and the full extent of behavioural overlap among reef herbivores.

6.3.1 Fine-scale understanding of the nutritional quality of corals as prey

The simplest optimal foraging models reduce prey consumption to a single currency, often long-term energetic gain (Houston and McNamara 2014), however in reality, each food item provides a variety of nutrients which must be balanced against one another (Simpson et al. 2004, Simpson and Raubenheimer 1993). Any robust predictions of dietary selection by corallivores will require an understanding of the variety of coral species preyed upon and the relative concentrations of different nutrients within their tissues. Recently, estimates for nutritional quality of corals have been limited in scope, evaluating corals at the genera level or using broad nutritional metrics (e.g. Graham 2007, Masterman 2012). Additionally, nutrient concentrations alone are not sufficient as the realized nutritional benefit for corallivore species consuming a given coral will also depend on differences in their gut morphology and digestion (Masterman 2012, Berumen et al. 2011), which may influence nutrient uptake (*sensu* Clements et al. 2016, in parrotfishes). A full investigation of each of these factors in tandem is needed to understand the energetic and nutritional pathways for post-bleaching mortality and sublethal effects among corallivores.

6.3.2 Understanding and functionally grounding coral-reef interaction networks

Limiting **Chapter 3** to just coral-corallivore interactions helped to focus clearly on the bottom-up effects of coral mortality. It also allowed for rapid collection of dietary data as coral and butterflyfish species identities can be determined quickly *in-situ*. However, there is immense value

in visualizing broader coral reef food webs, and recent advances make this a possible direction for future research. Bleaching-induced changes in fish diets foraging behaviour identified here (as well as the broader effects of coral bleaching and mortality) are likely to substantially affect interactions beyond the coral-corallivore system. Coral reefs are known to be incredibly diverse and complex (Reaka-Kudla 1997), including a variety of small cryptic organisms whose interactions are critical to reef energy budgets (Brandl et al. 2018). However, the overall structure of coral reef networks is relatively unknown, and this makes it difficult to predict how disturbances will propagate throughout coral reef food webs (Loreau et al. 2001). Recent advances in gut content metabarcoding make it possible to reveal the complexities of coral reef feeding interactions (Casey et al. 2019). These techniques now provide an exceptional opportunity to evaluate the effects of coral bleaching and mortality on food web structure, and this is a major component of my planned postdoctoral research. I hope to use gut content metabarcoding to reconstruct healthy and disturbed coral reef networks, compare differences in their topology, and investigate the relative strength and diversity of their contributions to essential coral reef functions (Brandl et al. 2019)

6.3.3 Broad assessment of behavioural overlap among herbivores

Chapter 5 highlights important differences in foraging behaviour between reef herbivores. Unfortunately, this study faced time limitations in the field, and because of the large amount of effort involved acoustically tracking each individual over several days, efforts were focused just on three of the most abundant species. However, herbivory on coral reefs is maintained by a diverse suite of organisms (Green and Bellwood 2009), and given the number of other different ways herbivores vary in foraging behaviour (Adam et al. 2018, Brandl and Bellwood 2014), the patterns of inter- and intraspecific variation in movement behaviour seen here are important to quantify

across the herbivores overall. A full understanding of the dietary and behavioural overlap would be valuable for management purposes (Chung et al. 2019).

6.4 Conclusion

In summary, this work highlights the importance of interspecific variance in foraging behaviour, as well as the importance of change in foraging behaviour as a result of bottom-up effects on food supply. Optimal foraging theory serves as a valuable tool to understand and predict bottom up effects, but there are a variety of reasons why optimal foraging responses may not occur as predicted. These changes in foraging behaviour can be critically important to the survival of the foragers themselves but may also have wide-reaching impacts that restructure ecological communities and alter important aspects of ecosystem functioning.

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Appendices

APPENDIX A: SUPPLEMENTAL MATERIAL

Ch2 Supplemental Material

Table S2.1 All papers used for quantitative analyses, the study taxon, and whether they observed a positive or negative relationship between food availability and the given foraging trait.

Citation	Trait	Species	Taxa	Response (N vs. P)
Pechacek and d'Oliere-Oltmanns (2004) *Biol. Conserv.*	Home Range	*Picoides tridactylus*	Birds	N
Palphramand et al. (2007) *Behav. Ecol. Sociobiol.*	Home Range	*Meles meles*	Mammals	N
Kubiak et al. (2017) *J. Zool.*	Home Range	*Ctenomys minutus*	Mammals	N
Combreau et al. (2000) *J. Arid Env.*	Home Range	*Chlamydotis macqueenii*	Birds	P
Combreau et al. (2000) *J. Arid Env.*	Home Range	*Chlamydotis macqueenii*	Birds	P
Chandler et al. (2016) *PLoS ONE*	Home Range	*Chaetodon triangulum*	Fish	N
Lehmann and Boesch (2003) *Behav. Ecol.*	Home Range	*Pan troglodytes verus*	Mammals	P
Campera et al. (2014) *Int. J. Primatol.*	Home Range	*Eulemur collaris*	Mammals	N
Hansen and Closs (2005) *Behav. Ecol.*	Home Range	*Galaxias argenteus*	Fish	N
Hansen and Closs (2005) *Behav. Ecol.*	Home Range	*Galaxias argenteus*	Fish	P
Hansen and Closs (2005) *Behav. Ecol.*	Home Range	*Galaxias argenteus*	Fish	P

Hansen and Closs (2005) *Behav. Ecol.*	Home Range	*Galaxias argenteus*	Fish	P
Marshall and Cooper (2004) *Ecology*	Home Range	*Vireo olivaceus*	Birds	N
Romanach et al. (2005) *J. Mammal.*	Home Range	*Geomys attaweri*	Mammals	N
Romanach et al. (2005) *J. Mammal.*	Home Range	*Geomys bursarius*	Mammals	N
Romanach et al. (2005) *J. Mammal.*	Home Range	*Thomomys bottae*	Mammals	P
Engstrom and Sanders (1997) *Wilson Bull.*	Home Range	*Picoides borealis*	Birds	N
Loveridge et al. (2009) *Ecography*	Home Range	*Panthera Leo*	Mammals	N
Li et al. (2014) *Mammalia*	Home Range	*Trachypithecus francoisi*	Mammals	N
Grueter et al. (2008) *Int. J. Primatol.*	Home Range	*Rhinopithecus bieti*	Mammals	P
Schmidt (2008) *Acta Theriol.*	Home Range	*Lynx lynx*	Mammals	N
Klein and Cameron (2012) *J. Mammlal.*	Home Range	*Peromyscus leucopus*	Mammals	N
Margalida et al. (2017) Ecol. Indic.	Home Range	*Gypaetus barbatus*	Birds	P
Winnie et al. (2008) *Ecology*	Home Range	*Syncerus caffer*	Mammals	N
Pejchar et al. (2005) *Ecol. Appl.*	Home Range	*Hemignathus munroi*	Mammals	N
Di Pierro et al. (2008) *Ecol. Res.*	Home Range	*Sciurus vulgaris*	Mammals	N
Di Pierro et al. (2008) *Ecol. Res.*	Home Range	*Sciurus vulgaris*	Mammals	N
Di Pierro et al. (2008) *Ecol. Res.*	Home Range	*Sciurus vulgaris*	Mammals	N
Bohr et al. (2011) *Int. J. Primatol.*	Home Range	*Microcebus griseorufus*	Mammals	N
Bohr et al. (2011) *Int. J. Primatol.*	Home Range	*Microcebus griseorufus*	Mammals	N
Lappan et al. (2017) *Anim. Behav.*	Home Range	*Symphalangus syndactylus*	Mammals	N

Dussault et al. (2005) *Can. J. Zool.*	Home Range	*Alces alces*	Mammals	P
Dussault et al. (2005) *Can. J. Zool.*	Home Range	*Alces alces*	Mammals	N
Zhou et al. (2011) *Int. Zool.*	Home Range	*Trachypithecus francoisi*	Mammals	N
Leiner and Silva (2007) *Acta Theriol.*	Home Range	*Marmosops paulensis*	Mammals	N
Redhead et al. (2016) *Ecol. Appl.*	Feeding Distance	*Bombus ruderatus*	Insects	N
Carvell et al. (2012) *Oikos*	Feeding Distance	*Bombus pascuorum*	Insects	N
Burkle and Montevecchi (2009) *J. Zool.*	Feeding Distance	*Uria aalge*	Birds	N
Vandenberghe et al. (2009) *Basic Appl. Ecol.*	Feeding Distance	*Anthus pratensis*	Birds	N
Britschgi et al. (2006) *Biol. Conserv.*	Feeding Distance	*Saxicola rubetra*	Birds	N
Tremblay et al. (2005) *Ibis*	Feeding Distance	*Parus caeruleus*	Birds	N
Bruun and Smith (2003) *Biol. Conserv.*	Feeding Distance	*Sturnus vulgaris*	Birds	N
Rauter and Reyer (1997) *Ibis*	Feeding Distance	*Anthus spinoletta*	Birds	N
López-Bao et al. (2014) *J. Anim. Ecol.*	Aggression	*Lynx pardinus*	Mammals	N
Powers and McKee (1994) *The Condor*	Aggression	*Lamporis clemenciae*	Birds	P
Powers and McKee (1994) *The Condor*	Aggression	*Lamporis clemenciae*	Birds	N
Crofoot (2007) *Behaviour*	Aggression	*Cebus capucinus*	Mammals	P
Smith et al. (2012) *The Condor*	Aggression	*Setophaga caerulescens*	Birds	P
Eide et al. (2004) *J. Anim. Ecol*	Aggression	*Alopex lagopus*	Mammals	N

Ch3 Supplemental Material

Figure S3.1 Map of Iriomote, Japan. Main panel shows Iriomote's location in the East China Sea, near Taiwan. Black circles on the inset indicate the three reef locations (from West to East): Sonai, Unarizaki, and Nata.

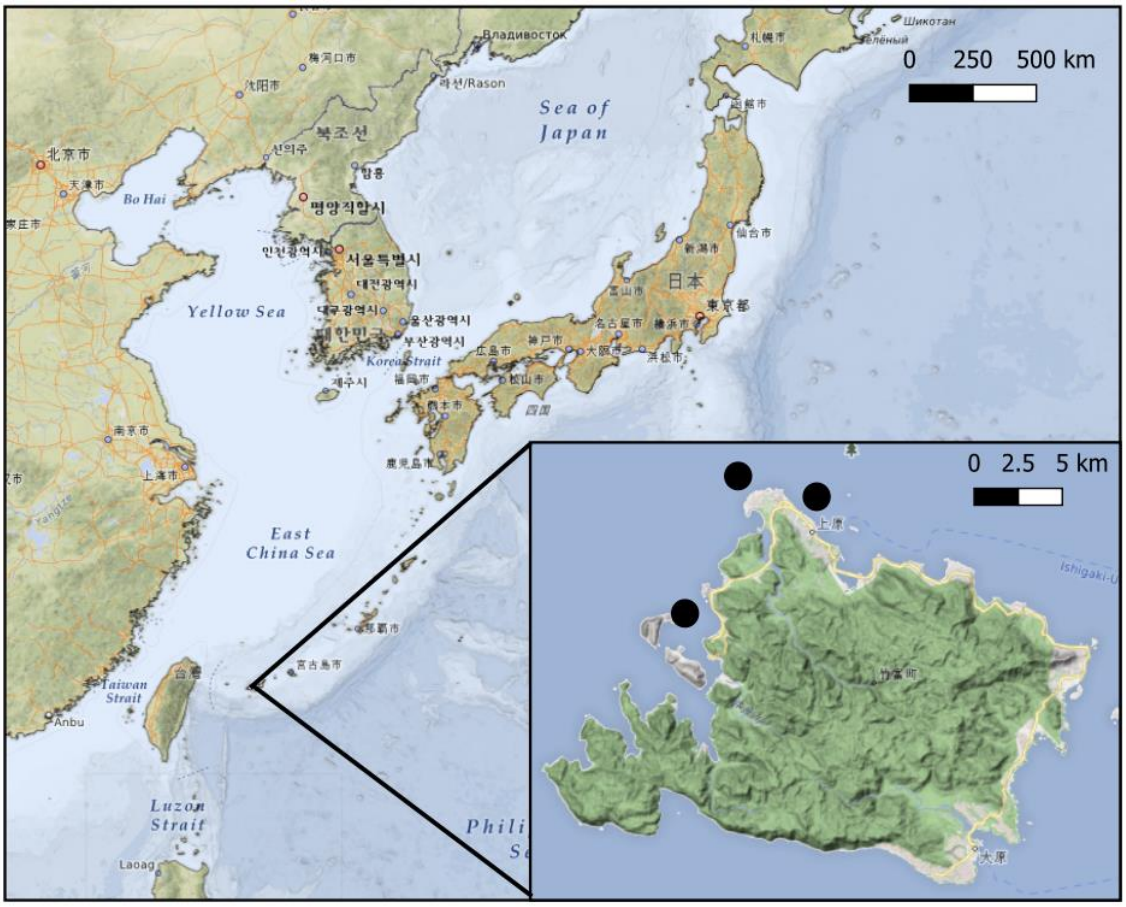

Figure S3.2 Hurlbert's Probability of Interspecific Encounter for A) the coral community, and B) butterflyfish diets, before and after bleaching. Dashed lines indicate the bleaching event. Blue represents these communities before bleaching, orange is after bleaching. Lettering above the box plots indicates significant differences among years.

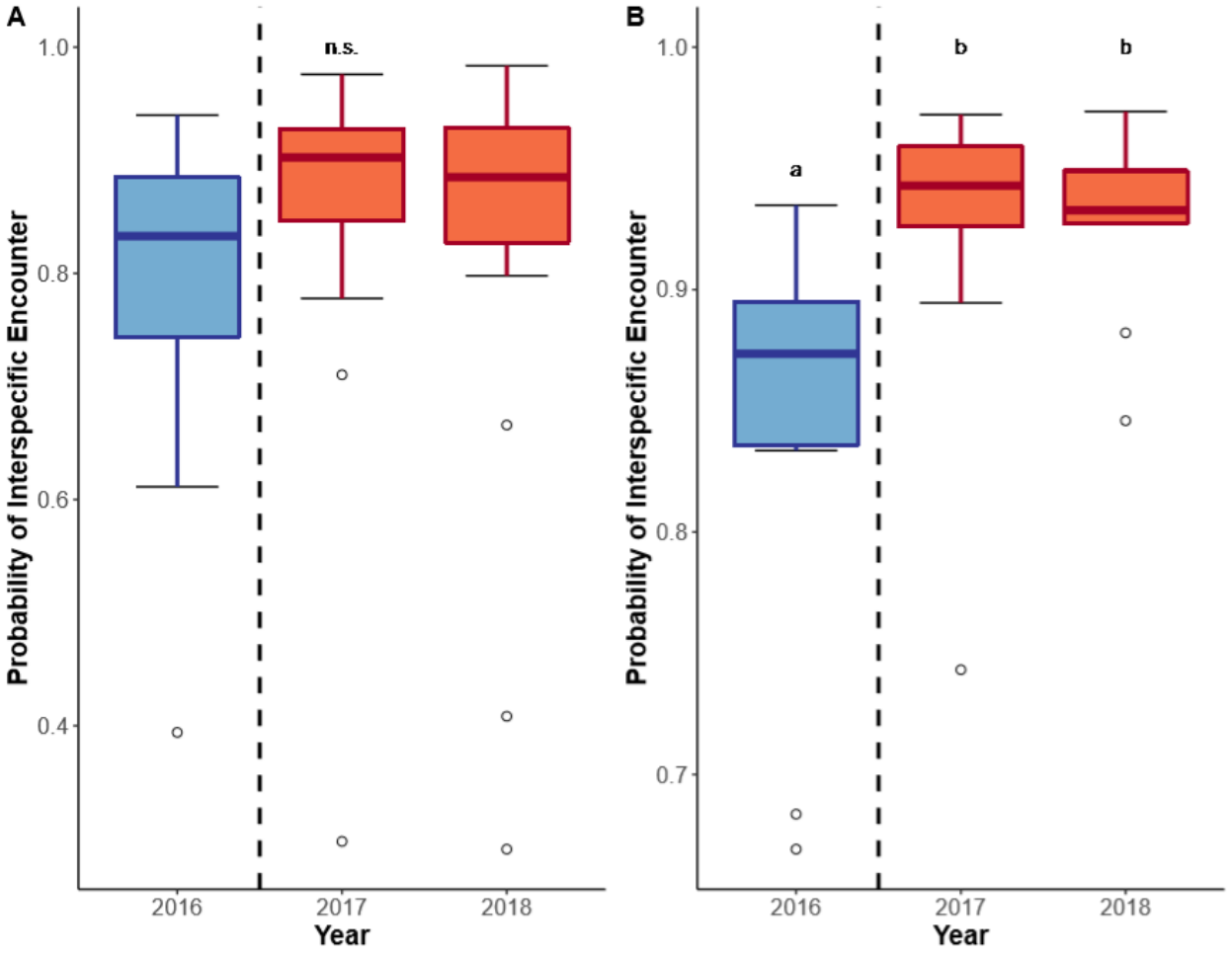

Figure S3.3 Null model analysis of network metrics. Comparisons of A) Alatalo Interaction Evenness, B) Shannon Diversity, C) Nestedness. Blue indicates a comparison before bleaching, red indicates after bleaching. Vertical lines indicate the observed network metric. Histograms represent predicted network metrics using reshuffled networks (method: vaznull).

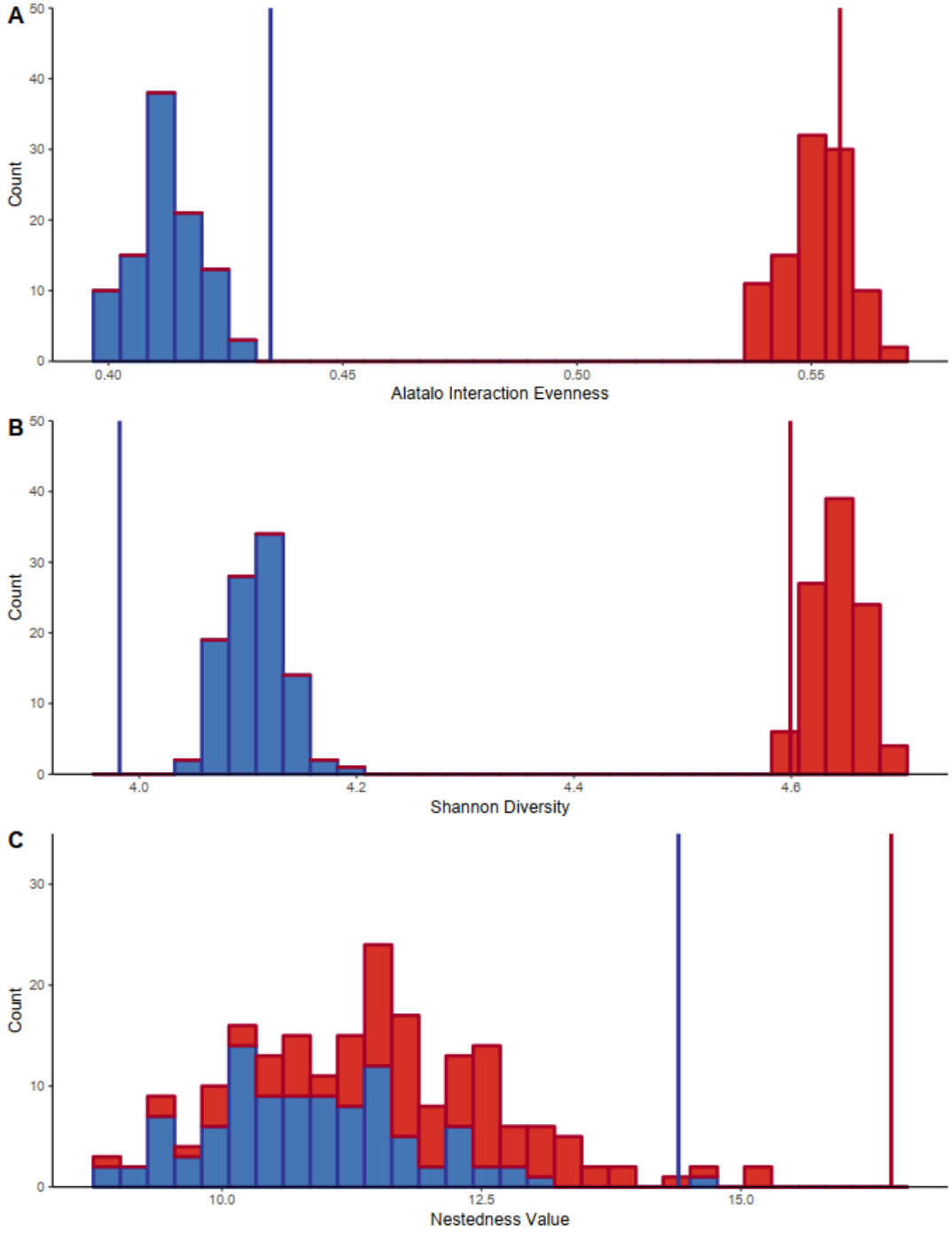

Table S3.1 Details of primary model selection. All models are GAMMs produced in package 'gammlss'. All contain two random intercept effects for fish identity of the two fish in each comparison.

Step	Model Description (Fixed Effects)	AIC
1)	Specialization ~ CoralCover + Species + Site + Year + Evenness	160.5073
2)	Specialization ~ CoralCover + Species + Year + Evenness	157.6594
3)	Specialization ~ CoralCover + Species + Evenness	156.115
4)	Specialization ~ CoralCover + Species	155.4499

Table S3.2 Total abundance of butterflyfishes (*Chaetodon spp.*) on transects over time.

Species	**2016**	**2017**	**2018**
C. argentatus	3	16	1
C. baronessa	0	2	0
C. bennetti	1	2	1
C. citrinellus	11	29	26
C. kleinii	3	2	0
C. lunulatus	115	110	42
C. melannotus	2	2	2
C. ornatissimus	4	8	3
C. plebeius	8	13	2
C. rafflesii	11	11	4
C. reticulatus	0	0	0
C. speculum	0	3	4
C. trifascialis	10	10	4
C. unimaculatus	7	15	13
All Species	**175**	**223**	**102**

Table S3.3 Observed network metrics before (2016) and after (2017 + 2018) coral mortality. All metrics calculated in package 'bipartite'.

	Before Disturbance	**After Disturbance**
Alatalo Interaction Evenness	0.43	0.56
Shannon Diversity	3.98	4.62
Connectance	0.22	0.25
Nestedness	14.36	15.07
H2'	0.39	0.32

Ch4 Supplemental Material

Figure S4.1 Comparison of model predictions between the formal analysis (A-C, random effect of fish ID), and this alternate set of models (D-F, random effect of fish ID + random effect of reef site). Note that a linear effect for coral cover was not included in the optimal model of bites per foray but is shown here (panel E) for direct comparison.

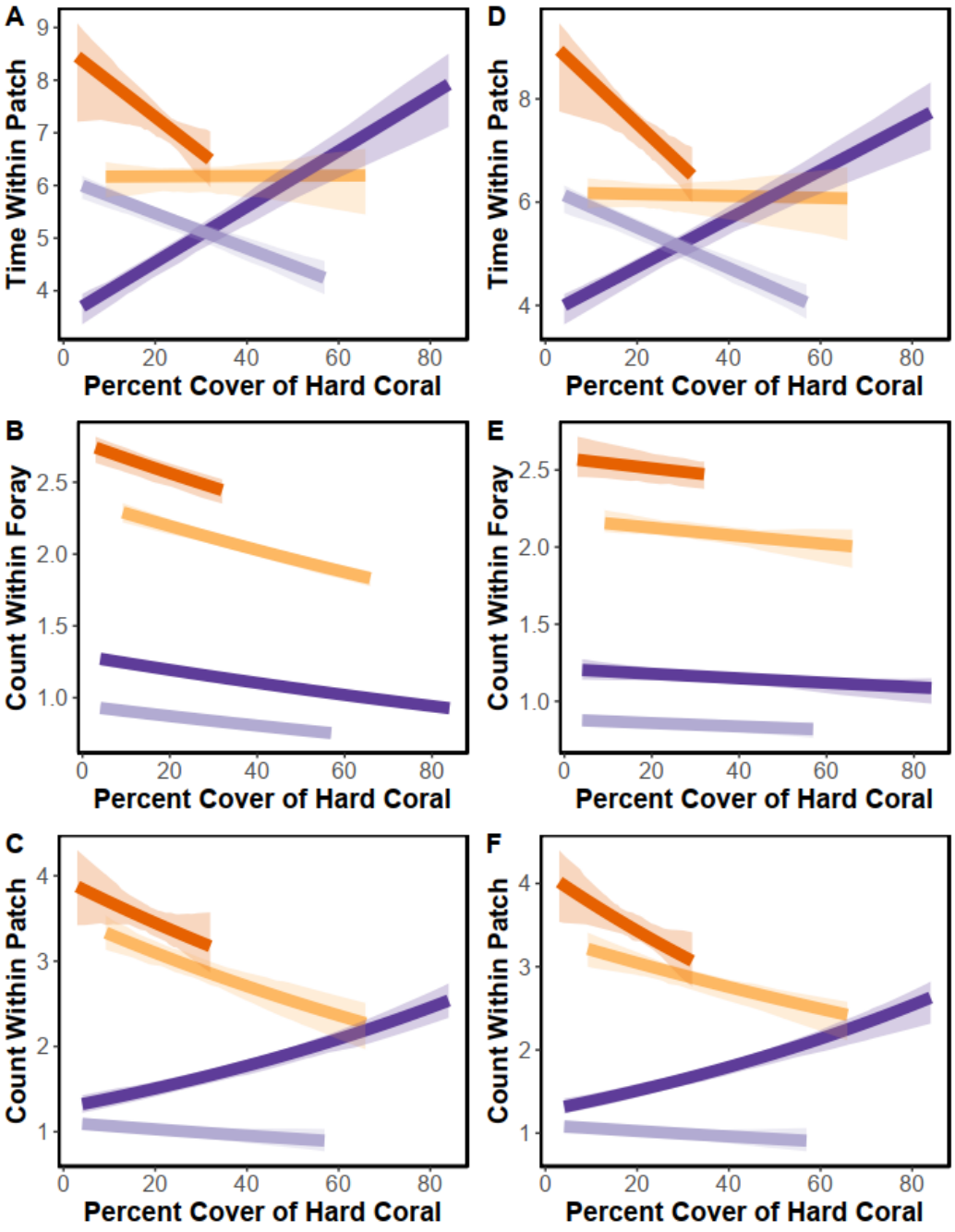

Table S4.1 Comparison of model fitting results between the formal analysis (random effect of fish ID), and this alternate set of models (random effect of fish ID + random effect of reef site). Optimal models for each are bolded and highlighted in light gray.

Trait	Candidate Model	AIC	
		Random Identity	Random Identity + Random Site
Residence Time	Time ~ Coral + Patchiness + Species	8853.8	8853.2
	Time ~ Coral + Species	8853.9	8853.3
	Time ~ Coral * Species	**8849.1**	**8847.2**
	Time ~ Species	8855.1	8852.6
	Time ~ Intercept Only	8860.2	8860.6
Movement Duration	Time ~ Coral + Patchiness + Species	12134.0	12129.6
	Time ~ Coral + Species	12132.9	12128.2
	Time ~ Coral * Species	12130.5	12139.3
	Time ~ Species	**12131.2**	**12126.8**
	Time ~ Intercept Only	12142.1	12139.3
Bites Per Foray	Bites ~ Coral + Patchiness + Species	8720.1	8713.3
	Bites ~ Coral + Species	**8721.0**	8714.5
	Bites ~ Coral * Species	8722.5	8716.8
	Bites ~ Species	8725.7	**8712.8**
	Bites ~ Intercept Only	8852.0	8849.9
Bites Per Patch	Bites ~ Coral + Patchiness + Species	6644.5	6645.3
	Bites ~ Coral + Species	6644.6	6645.0
	Bites ~ Coral * Species	**6640.3**	**6640.7**
	Bites ~ Species	6644.7	6645.2
	Bites ~ Intercept Only	6736.2	6738.2

APPENDIX B: PAPERS ARISING FROM THIS THESIS

Semmler, R.F, Brandl, S.J., Keith, S.A., and D.R. Bellwood (2021) Fine-scale foraging behaviour reveals differences in the functional roles of herbivorous reef fishes. *Ecology & Evolution* DOI: 10.1002/ece3.7398.

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ORIGINAL RESEARCH

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Fine-scale foraging behavior reveals differences in the functional roles of herbivorous reef fishes

Robert F. Semmler[1] | Simon J. Brandl[2,3,4] | Sally A. Keith[1] | David R. Bellwood[3,4]

[1]Lancaster Environment Centre, Lancaster University, Lancaster, UK

[2]Department of Marine Science, Marine Science Institute, University of Texas Austin, Port Aransas, TX, USA

[3]ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

[4]College of Science and Engineering, James Cook University, Townsville, QLD, Australia

Correspondence
Robert F. Semmler, Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK.
Email: rsemmler37@gmail.com

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Abstract

Efforts to understand and protect ecosystem functioning have put considerable emphasis on classifying species according to the functions they perform. However, coarse classifications based on diet or feeding mode often oversimplify species' contributions to ecological processes. Behavioral variation among superficially similar species is easily missed but could indicate important differences in competitive interactions and the spatial scale at which species deliver their functions. To test the extent to which behavior can vary within existing functional classifications, we investigate the diversity of foraging movements in three herbivorous coral reef fishes across two functional groups. We find significant variation in foraging movements and spatial scales of operation between species, both within and across existing functional groups. Specifically, we show that movements and space use range from low frequency foraging bouts separated by short distances and tight turns across a small area, to high frequency, far-ranging forays separated by wide sweeping turns. Overall, we add to the burgeoning evidence that nuanced behavioral differences can underpin considerable complementarity within existing functional classifications, and that species assemblages may be considerably less redundant than previously thought.

KEYWORDS

complementarity, coral reefs, foraging behavior, functional traits, movement

1 | INTRODUCTION

Understanding how, why, and when different species contribute to essential ecosystem functions has gained increased focus in recent years, with the aim to both advance fundamental knowledge and improve management (Bellwood et al., 2019; Díaz & Cabido, 2001; Folke et al., 2004; Tilman et al., 1997). For both fundamental and applied research, it is not only important to identify species that are key to the maintenance of essential functions, but also to establish the extent to which species are functionally similar (underpinning redundancy) or different (underpinning complementarity) (Blüthgen & Klein, 2011; Brandl et al., 2019; Burkepile & Hay, 2011; Frost et al., 1995; Lawton & Brown, 1993; Nyström, 2006). Complementarity essentially describes niche partitioning

Robert F. Semmler and Simon J. Brandl shared first-authorship

in an Eltonian, functional context (Bellwood et al., 2019; Brandl et al., 2019). Substantial complementarity has been documented within superficially homogeneous groups of flying insect pollinators (Blüthgen & Klein, 2011), grazing subtidal urchins (Brandt et al., 2012), savannah ungulates (Pringle et al., 2014), and small desert herbivores (Thibault et al., 2010). However, for practical purposes a delicate balance is necessary between the benefits of tractability and the risks of oversimplification. On the one hand, it is necessary to ensure tractability or utility of functional groups, which requires collapsing diverse species into groups of ecologically similar entities, for example, trophic groups or guilds. On the other hand, groupings may oversimplify ecological dynamics, masking important differences between species within the same functional category and their contributions to ecological processes (Körner, 1994).

Ecosystems with high inherent species richness, such as coral reefs and tropical rainforests are characterized by a complex mosaic of biological interactions, and a wide variety of available of microhabitats (Gentry, 1982; Graham & Nash, 2013; Reaka-Kudla, 1997). This complexity has spurred the development of functional group classifications, on coral reefs in particular (Bellwood et al., 2004; Darling et al., 2012; Nyström, 2006). Nevertheless, species within these groups may differ in a number of ways that could impact the delivery of their functions. Thus, to ensure that functions are maintained as species assemblages change, we need to know the extent to which species within the same broad functional entity differ from one another. It is doubtful that there is "true redundancy" within functional groups; rather there will be some degree of complementarity, dependent on the scale at which behavior is assessed (Brandl & Bellwood, 2014). Within functional entities, complementarity of functional delivery can be a result of fine-scale partitioning of resources, which can be based on species-specific differences in targeted resources, or temporal and spatial patterns in their exploitation (Fründ et al., 2013; Wellborn & Cothran, 2007). Species foraging patterns are likely to reflect all of these elements, thus providing a window into the extent of functional complementarity among species.

Foraging movements are determined by economic decisions to optimize the food resource gained per unit of energy expended (MacArthur & Pianka, 1966). Thus, while not the only factors affecting movement, foraging movements depend both on dietary preferences and the abundance and patchiness of the food resources targeted (Stephens & Krebs, 1986). For example, to account for long travel times and their associated costs, patchy food resources require long patch residence times (Charnov, 1976). Additionally, low-quality patches will be depleted quickly below an energy gain per unit effort that maintains optimum foraging (McNair, 1982). As a result, species that focus their diets on patchy or lower quality food items may have shorter patch residence times and greater exploration times (Stephens & Krebs, 1986). Because foraging movement decisions are made based on the density and location of food resources, even among closely related species, these types of small differences in dietary preference can favor different foraging strategies (Pyke, 1984). In addition to these factors, patch use may also be impacted by the threat of predator (Brown et al., 1992; Catano et al., 2015) or competitor species (Mitchell et al., 1990).

Variations in foraging strategy are the result of adaptive changes that facilitate coexistence among species competing for space and resources (Chesson, 2000; Tilman, 1982). However, different foraging strategies are also likely to affect the spatial extent over which species perform their role (Nash et al., 2013, 2016). Efforts to identify a forager's spatial scale of operation through home-range assessments are useful but feeding activity can be heterogenous and concentrated within certain areas of the animal's range (Streit et al., 2019; Welsh & Bellwood, 2012). As a result, assessments of animals' foraging movements can benefit from various types of behavioral observations across multiple spatial and temporal scales.

Coral reef fishes can overlap heavily in their broad use of habitats and in their contributions to ecosystem functions (Mouillot et al., 2014). Conservation actions have been adopted on the basis of these strategies to manage coral reef ecosystems with a particular focus on the role of herbivorous fishes (Adam et al., 2015a, 2015b; Chung et al., 2019; Green & Bellwood, 2009). Herbivory by coral reef fishes was originally divided into four broad functional categories based on foraging strategies: grazers, browsers, scrapers, and bioeroders (Bellwood et al., 2004; Green & Bellwood, 2009; Nyström, 2006). These categories cover a suite of functions that facilitate reef resilience to disturbance, and can prevent them from shifting to less desirable, alternate states dominated by algae (Hughes et al., 2007). However, species within these groups are far from homogenous in their niches (Bellwood et al., 2019; Brandl et al., 2019). For example, browser species can differ strongly in their preference for algal food resources (Puk et al., 2016; Rasher et al., 2013; Streit et al., 2015), while grazers separate into species targeting the tips of algae (e.g., croppers) and species targeting particulate matter within algal turfs (e.g., Brandl & Bellwood, 2016; Tebbett et al., 2017). Similarly, scraping and bioeroding parrotfishes differ substantially in their ingestion and postingestion treatment of resources (Adam et al., 2018; Clements et al., 2016; Nicholson & Clements, 2020), leading to various refinements of the initial categories over the years (Brandl & Bellwood, 2016; Siqueira et al., 2019). However, these classifications still focus primarily on diet and resources acquisition method. Few consider spatial dimensions of resource use. While reef herbivores are known to vary in their specific microhabitat use (e.g., horizontal, vertical, underside) (Adam et al., 2018; Brandl & Bellwood, 2014; Fox & Bellwood, 2013; Puk et al., 2020), fine-scale foraging movements and spatial resource partitioning in coral reef fishes remains poorly understood (Streit et al., 2019). Yet it is at this scale that resource partitioning and complementarity may be most strongly expressed, with significant effects for reef functioning (Ruttenberg et al., 2019).

We investigate the degree to which differences in foraging behavior can transcend boundaries set by traditional functional group classifications. Specifically, we assess the fine-scale foraging movements of three coral reef herbivores: two grazer/cropper species (*Siganus corallinus* and *Siganus vulpinus*) and one scraper (*Scarus schlegeli*). We ask: How does foraging behavior and space use vary

between species? Specifically, (a) which traits (speed, turning angle etc.) define the differences between their foraging paths? (b) Do short-term hourly movement patterns (in situ behavioral observations) reflect longer-term daily patterns of space use (assessed via active acoustic telemetry)? (c) Are there substantial differences in the scale of operation among species, and does this affect the spatial extent over which these species perform their functional role?

2 | METHODS

Field sites were located on reefs at Lizard Island, a granitic mid-shelf island on the Great Barrier Reef. We studied three species: two rabbitfishes *Siganus vulpinus* and *Siganus corallinus* (Figure 1), and one parrotfish *Scarus schlegeli*. The two rabbitfishes are categorized as cropping herbivores that take discrete bites from small algae or cyanobacteria (i.e., grazers) (Brandl & Bellwood, 2016; Hoey et al., 2013) and occur almost exclusively in stable pairs (Brandl & Bellwood, 2013; Brandl & Bellwood, 2015). By contrast, *Scarus schlegeli* lives in small groups and is a scraping herbivore that ingests the entire epilithic algal matrix (i.e., scraper) (Clements et al., 2016). While the vast majority of grazing herbivores on reefs have limited home ranges and exhibit strong site fidelity at the reef scale, there is considerable variation in the movements among both rabbitfishes (Brandl & Bellwood, 2013; Fox & Bellwood, 2011) and parrotfishes (Welsh & Bellwood, 2011, 2012). The three species in the present study were selected to permit a comparison between two species commonly considered to be functionally equivalent (the two cropping rabbitfishes), while anchoring these observations within the broader classification of grazing herbivores by including a functionally different species (the scraping parrotfish). Foraging path observations were performed on Big Vicki's Reef (5 hectares) from February 7th to February 11th 2014, while the acoustic tracking was performed on Watson's Reef (2 hectares) from April 25th to May 4th 2012. Both reefs are on the leeward side of the island and represent typical backreef sites with low wave energy and depths between 2 and 5 m. The two reefs are separated by a distance of approximately 2 km and represent broadly similar lagoonal habitats dominated by corals and turf algae. We chose to perform the two parts of the study on different reefs for several reasons: (a) since acoustic tracking involves the capture and manipulation of fishes, which may modify the individual's reactions to observers in the water, we considered it safer to avoid the reef that fishes were tagged on; (b) Big Vicki's reef offered a more expansive and slightly deeper reef environment, thus allowing for higher replication without the risk of re-sampling the same individuals, while ensuring a minimal observer effect from the snorkeler in the water.

FIGURE 1 Photo of two *Siganus corallinus* individuals (credit: Victor Huertas)

2.1 | Focal foraging path observations

We quantified the fishes' foraging movements in situ. A single snorkeler (SJB), equipped with a handheld global positioning system (GPS) unit in a waterproof case, which was set to automatically record its position every 5 s, performed the observations. We opportunistically located an adult of one of the three target species and followed the fish for 30–45 min. We followed the fish as closely as possible (snorkeling offering one of the least disturbing methods of observation; Welsh & Bellwood, 2011), recording different behaviors (i.e., swimming and feeding behavior). For each behavior, the observer recorded the exact time of the event (hh:mm:ss) using a digital wristwatch that was precisely synchronized with the GPS unit. All focal observations occurred between 08:00 and 17:00, a time window during which most herbivorous fish species are actively foraging. We considered a foraging bout to be finished once the fish stopped biting the substratum and assumed a horizontal position characteristic of swimming activity (Nash et al., 2012). During all observations, we ensured positioning directly above the focal individual (which restricted our observations to areas with depths >2 m to ensure fishes were undisturbed by the observer). After 30–45 min (or when the focal individual showed signs of behavioral modification due to being followed by the snorkeler or contact was lost due to depth or visibility), the observer abandoned the focal individual in search of an individual of one of the other two species. Once individuals in all three species were followed, the observer took a haphazard turn, swam for at least 100 m, and searched for another individual in any of the three target species. To avoid duplication, we spread efforts across different sections of the reef and took notes on size and color patterns of the observed fish.

2.2 | Acoustic telemetry

To obtain a more detailed assessment of space use in the two rabbitfish species, we used active acoustic telemetry on five adult individuals of *Siganus corallinus* (in three pairs; SC1 and SC2, SC4, SC5, and SC6) and three adult individuals of *Si. vulpinus* (in two pairs; SV2, SV3 and SV4). An additional individual was tagged in each species but disappeared shortly after release, probably due to predation (Khan et al., 2016). While the behavior of paired individuals will not

be wholly independent from their partner, separation of individuals or exclusive treatment of only one partner can result in changes of behavioral patterns. To tag the individuals, we caught pairs using barrier nets on Watson's Reef and transported them immediately to Lizard Island Research Station in large bins full of fresh seawater, ensuring pairs were maintained. At the station, we placed pairs in separate large (300 L) flow-through seawater aquaria. In the evening of the day of capture, we anesthetized each fish in a saline solution of tricaine methanesulfonate (MS-222, 0.13 g/L) and surgically implanted an acoustic transmitter (Vemco V9-6L) into the gut cavity (cf. Brandl & Bellwood, 2013). After closing the incision with sutures and ensuring full recovery from anesthesia, we held fishes in their tanks overnight. We returned the fishes to the exact site of capture the next morning.

Fish were allowed 48 hr to recover, after which we started acoustically tracking each fish from a 3.1 m kayak using a calibrated directional hydrophone (VH110) and an acoustic receiver (VR100, both Vemco) (Brandl & Bellwood, 2013; Fox & Bellwood, 2011). Tracking continued from 30 min before dawn to 30 min after dusk (approx. 06:30–18:00). We maneuvered the kayak to obtain maximum signal strength from the respective tag every 15 min, while the receiver recorded the kayak's GPS position. We tracked each fish for three nonconsecutive days and verified the identity and normal behavior of the tracked individual via a short in situ validation by a snorkeler each day (identifying the tagged fishes through the visible surgical incision; Brandl & Bellwood, 2013).

2.3 | Data analysis

We performed all data analyses in R (R Core Team, 2019). For the snorkeler-based observations, we matched timed GPS recordings with recorded times for each feeding event to quantify the path between successive feeding events for each. From these, we calculated six traits to characterize different aspects of foraging behavior or space use: (a) 95% minimum convex polygon (MCP) of space used during the observation, (b) mean swimming speed, (c) mean turning displacement (higher displacement = sharper turns) between successive movement bearings, (d) overall tortuosity of the feeding path, (e) number of feeding events per minute, and (f) average distance between feeding events (interforay distance). We computed MCPs using the package *adehabitatHR* (Calenge, 2006), and distances (using the Haversine method) and bearings between points, using the package *geosphere* (Hijmans, 2016). We calculated overall path tortuosity as the ratio of the straight-line distance between the start and end locations, and the total distance travelled by the fish (following Fulton & Bellwood, 2002; Secor, 1994). We tested for differences between the three species in each of these traits with Analyses of Variance (ANOVA). To ensure normality and homoscedasticity of variances, it was necessary to log transform the MCP values. After transformation, MCP values for *Si. vulpinus* became normally distributed (Shapiro–Wilk: 0.88, $p = 0.12$) and MCP variance among species was homogenous (Bartlett: 5.64, $df = 2$, $p = 0.06$).

Furthermore, we visualized inter- and intraspecific variation in these traits with a nonmetric multidimensional scaling (MDS) ordination based on a Bray–Curtis dissimilarity matrix (Gauch, 1973). We ran the ordination on a square root Wisconsin transformed matrix to ensure that differences in scale between trait values did not influence the analysis (Del Moral, 1980). We used a Permutational Analysis of Variance (PERMANOVA) to test for significant differences in the overall foraging strategies of the three species and tested for homogeneous multivariate dispersion between species using PERMDISP. Lastly, we used the SIMPER analysis to determine which traits contributed most to differences in foraging behavior between species. PERMANOVA, PERMDISP, and SIMPER tests were run on the transformed dissimilarity matrix using the package *vegan* (Oksanen et al., 2016).

For the active tracking data, we used the GPS points from each 15-min intercept (choosing the highest-strength signal around the 15-min mark) to compute kernel utilization distributions (KUDs) for each individual, which we used to estimate 95% daily foraging areas and 50% core areas for each individual (Brandl & Bellwood, 2013). We calculated KUDs for each day and the cumulative GPS points across all days. We again used the package *adehabitatHR* (Calenge, 2006). We tested differences in cumulative daily foraging areas and core areas between the two rabbitfishes with two-sample *t* tests.

Lastly, we also computed overall feeding rates (bites/min) and movement rates (meters/min) for each fish observed on snorkel. Specifically, our rationale was that differences in foraging strategy between species may be underpinned by fine-scale dietary differences. Differences in feeding efficiency between species may help to highlight this, as diets may provide more or less energy per bite. Feeding rates were calculated based on the total time spent feeding within each observation (with each feeding event estimated as 5 s), multiplied by previously established bite rates during feeding events, for each species (Brandl & Bellwood, 2014). Feeding efficiency was calculated by dividing each individual's feeding rate by its movement rate. As with the six traits above, for these three factors we tested differences between species with ANOVA.

3 | RESULTS

Overall, we followed 29 individual fishes (counts: *Siganus corallinus* = 9 individuals; *Si. vulpinus* = 10 individuals; *Scarus schlegeli* = 10 individuals). Overall observation time totaled 17.4 hr (mean observation times: *Siganus corallinus* = 35.9 min ± 2.21 SE; *Si. vulpinus* = 34.5 min ± 2.54; *Scarus schlegeli* = 37.4 min ± 1.82) during which we recorded 1,190 feeding events. Foraging patterns differed for the three fish species, both within and across functional group boundaries. Variation in short-term foraging movements (Figure 2) was mirrored by daily space use in the two rabbitfishes, where both 95% daily foraging areas and 50% core areas of *Si. vulpinus* were significantly larger than those of *Si. corallinus* ($t(6) = -6.00$, $p < 0.001$, and $t(6) = -6.28$, $p < 0.001$, respectively) (Figure 3). Overall, we found significant variation between species for five of the six movement

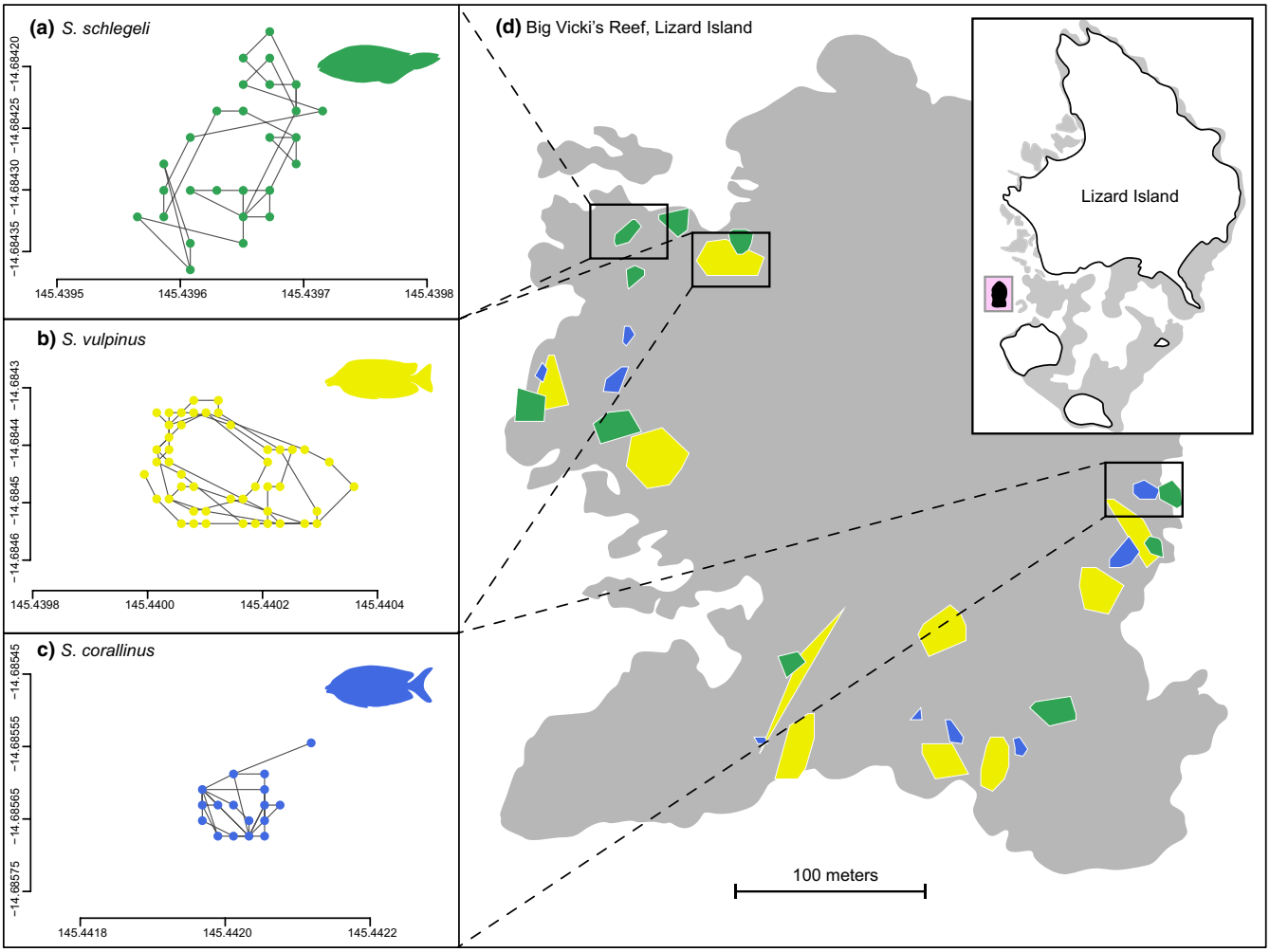

FIGURE 2 Foraging paths and resulting size and distribution of short-term feeding areas (direct observation). (a–c) Example foraging paths for all three species. Green = the parrotfish *Sc. schlegeli*, yellow and blue = the rabbitfishes, *Si. Vulpinus*, and *Si. corallinus*, respectively. Dots represent foraging locations, while lines represent vectors between foraging events. Path insets not scaled by area, but relative size can be seen in the wider figure. (d) Distribution of feeding areas (MCP) for each species on Big Vicki's Reef with inset showing location of Big Vicki's Reef on Lizard Island, colors as above

traits we investigated (Figure 4). Specifically, there were significant differences in the log of foraging area covered ($F_{2,26} = 21.96$, $p > 0.001$), mean speed of travel ($F_{2,26} = 3.98$, $p = 0.031$), mean turn angle ($F_{2,26} = 4.71$, $p = 0.018$), feeding frequency ($F_{2,26} = 9.44$, $p > 0.001$), and mean interforay distance ($F_{2,26} = 7.41$, $p = 0.003$). *Si. corallinus* had the smallest mean foraging area, while *Si. vulpinus* had the largest. We found a similar relationship for mean speed, with *Si. vulpinus* travelling at greater speeds than *Si. corallinus*. *Si. vulpinus* also took wider turns between feeding bouts compared to *Si. corallinus* and *Sc. schlegeli* (Figure 4). However, despite difference in turning angles, we found no significant differences for the overall tortuosity of foraging paths. While mean tortuosity did not differ, variance in path tortuosity was substantially larger for the rabbitfishes than for *Sc. schlegeli*. *Sc. schlegeli* had more frequent foraging bouts than *Si. corallinus*, and *Si. vulpinus* had longer interforay distances than either of the other species.

As would be expected from the results above, species identity was significant in determining foraging behavior, explaining 42% of variance among individuals ($R^2 = 0.42$, $p < 0.001$, Figure 5). All species showed similar levels of intraspecific variability in foraging traits; multivariate dispersions were not significantly different between species ($p = 0.060$). Despite not differing significantly in the univariate analysis, path tortuosity contributed to differences between species within the multivariate analysis. Differences between species were most strongly predicted by the size of their foraging areas, the tortuosity of their foraging paths and the mean turning angle between feeding events, with each of these traits explaining over 20% of the difference between any two species. Mean speed was the least informative trait, explaining <10% of the average difference between any two species. Differences between the parrotfish *Sc. schlegeli* and the rabbitfish *Si. corallinus*, were mostly driven by a tighter (18%), smaller (19%) and more tortuous feeding path (24%) for the rabbitfish. Similar differences were reflected between the two rabbitfish, with large proportions of variance defined by tighter turns (26%), and a smaller feeding area (29%) for *Si. corallinus*, however a less tortuous path (20%) than *Si. vulpinus*. Differences

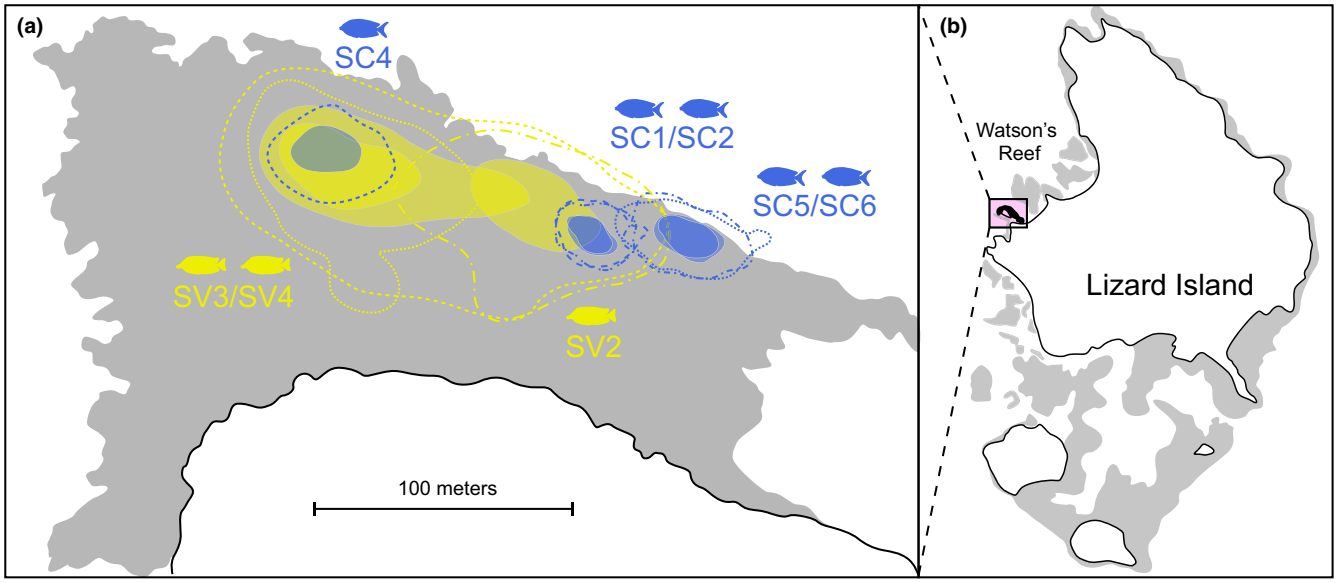

FIGURE 3 Relative size of daily foraging areas (acoustic telemetry). (a) Spatial distribution of daily foraging areas on Watson's Reef. Dotted and dashed lines mark the 95% Kernel Utilization Distributions (KUDs), while filled, transparent areas mark the 50% core areas. Fish numbers are given for all paired and the two singular individuals. Colors as above. (b) Location of Watson's Reef on Lizard Island

between *Sc. schlegeli* and *Si. vulpinus* were also most strongly determined by a larger (19%) more tortuous feeding path (21%) for the rabbitfish, as well as a faster feeding frequency (21%) for the parrotfish.

Lastly, species differed significantly in their feeding rates ($F_{2,26} = 44.55$, $p > 0.001$), movement rates ($F_{2,26} = 4.33$, $p = 0.024$), and their resulting feeding efficiency ($F_{2,26} = 12.71$, $p > 0.001$) (Figure 6). *Si. corallinus* had the lowest movement rates, with both *Si. vulpinus* and *Sc. schlegeli* moving faster. Based on unique foraging events and bite rates, the parrotfish took many more bites per minute than either rabbitfish species. Due to these differences, the feeding efficiency of the parrotfish was higher than either rabbitfish. While across the three species, a positive relationship between movement and bite rates was visible, only *Si. corallinus* showed an intraspecific trend where individuals traveling farther took more bites per unit time.

4 | DISCUSSION

Categorization of species based on their functional roles is a useful concept in ecology and conservation. However, behavioral differences among species within the same group may result in functional variation that is unaccounted for in broad categories. Our results demonstrate behaviorally mediated diversity in functional roles of herbivorous fishes within and across functional groups, resulting in complementarity in their niches and spatial differences in the delivery of their functional roles. The differences in fine-scale foraging paths of the grazers, *Si. corallinus* and *Si. vulpinus*, are reflected in their broad-scale, reef-scape movements. Both fine-scale activities and sustained broad-scale movements are critical components of animals' energy budgets, but they also shape their functional roles within ecosystems, especially in a spatial context.

In our analysis, we found clear differences in foraging behavior between the three fish species, even those within the same functional group and genus, that is, grazing rabbitfish. Feeding frequency was the primary trait that differentiated the two functional groups, both in terms of the number of forays per minute and the number of bites per minute. This difference could be expected as scrapers primarily remove epithelial algal matrix from flat or convex surfaces, which can be more readily located without disrupting movement (Brandl & Bellwood, 2014; Clements et al., 2016). The two grazers, on the other hand, will inspect holes or crevices for patches of algae to crop (Brandl & Bellwood, 2015; Fox & Bellwood, 2013), leading to slower bite rates and less frequent feeding events. As a result of its fast feeding rate and intermediate movement rate, the parrotfish appears to be the most efficient, or least selective, forager, taking the largest number of bites while traveling only short distances between those bites.

As well as the expected behavioral differences between functional groups (i.e., grazers vs. scrapers), there were substantial differences between the two grazers. *Si. corallinus* moved slowly, focusing feeding effort within a very small area of the reef, and took sharp turns to stay within this core area. In contrast, *Si. vulpinus* ranged widely over a considerably larger feeding territory and travelled substantial distances between forays in a roughly circular, and remarkably predictable pattern. Though sample sizes for acoustic tracking were limited and included nonindependent paired individuals, we have considerable confidence that these differences were reflected in the daily foraging areas of each species as well, with *Si. corallinus* occupying a much smaller foraging area than *Si. vulpinus*. Complementary scales of space use among these two species indicate that both species will contribute more strongly to algal grazing

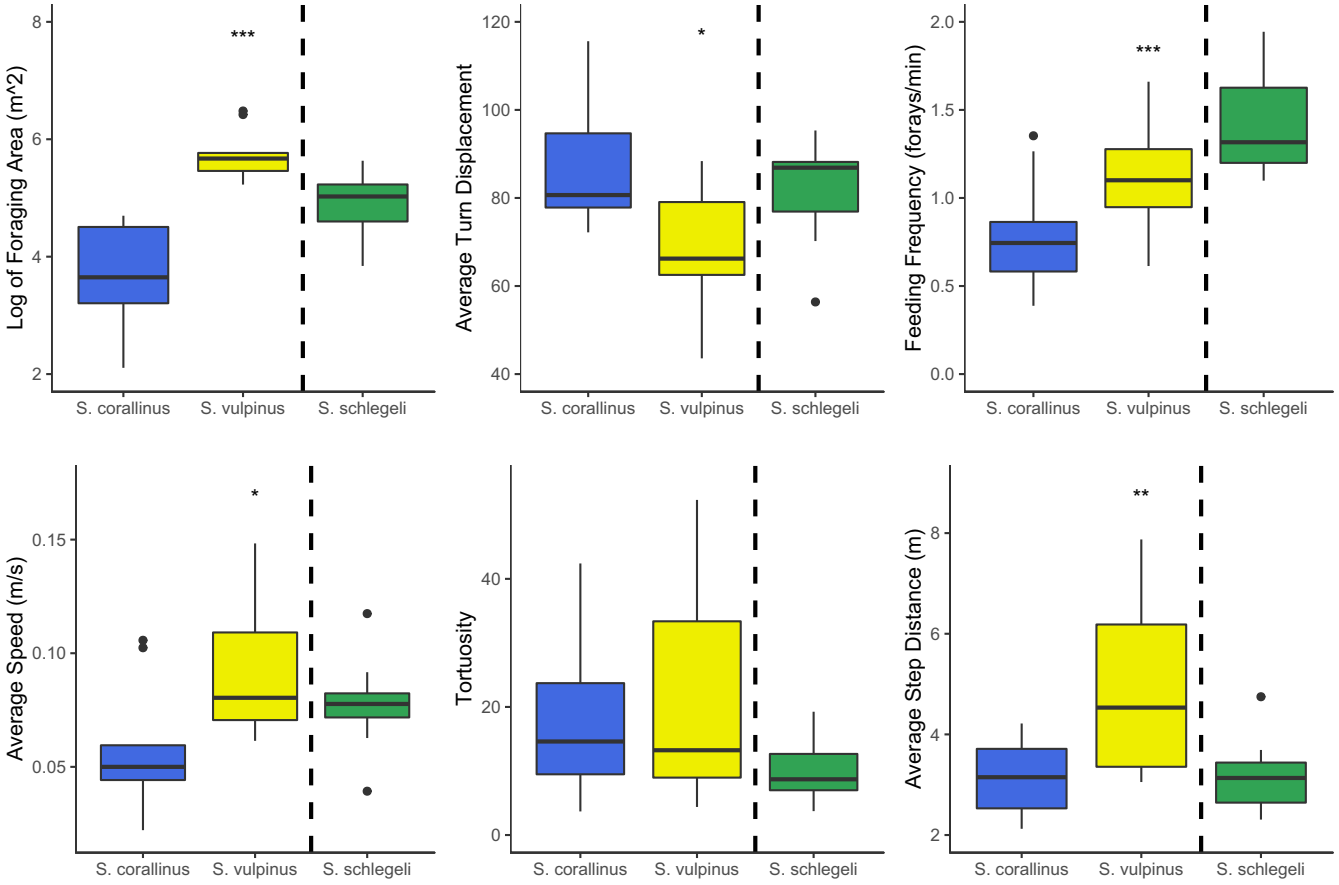

FIGURE 4 Differences in the six metrics used to evaluate foraging paths of the three species. Asterisks indicate significant differences among species via ANOVA. *Si. vulpinus* foraging movements are characterized by: large areas, wide turns, higher speeds, and longer interforay distances; *Si. corallinus* foraging movements are characterized by: small areas, sharp turns, low feeding frequency, low speed, and short interforay distances; *Sc. schlegeli* occupy intermediate positions but display the highest frequency of foraging. Boxplots represent the median and interquartile range of each foraging trait. Dashed lines separate the two grazing rabbitfishes from the scraping parrotfish

than either could alone, which holds important implications for the management of herbivory on coral reefs (Topor et al., 2019).

Some of the differences in the foraging search patterns of the rabbitfish species could be driven by differences in their diets. While both are considered grazers, *Si. corallinus* primarily targets small, dense red algae, while *Si. vulpinus* mostly consumes cyanobacteria (Hoey et al., 2013). Furthermore, *Si. vulpinus*, with its extremely elongated snout, appears to obtain most of its food from deep crevices and interstitial microhabitats compared to *Si. corallinus*, which targets shallower crevices that it can exploit with its more moderate head morphology (Brandl & Bellwood, 2014, 2016). Differences in foraging behavior between the two species may be driven by the spatial organization of these resources on reefs and their patchiness; while small red algae and shallow crevices can be expected to occur frequently throughout the reef matrix, deeper crevices with dense mats of cyanobacterial growth are less common (Brandl, Robbins, & Bellwood, 2015; Harris et al., 2015). These differences closely resemble those recorded in a range of wrasse species on coral reefs (Fulton & Bellwood, 2002). Additionally, cases of food distribution affecting foraging strategies, like those seen here, have been seen in a variety of systems, including ant colonies (Lanan, 2014). However, we currently lack detailed information on the spatial organization of algal resources needed to determine the exact relationships between resource distributions and the fishes' foraging movements. Differences in foraging paths may be influenced by many aspects of the targeted food resources, including their patchiness, within patch density, or their nutritional and energetic quality (Schatz & McCauley, 2007).

While both red algae and cyanobacteria are thought to be nutritionally poor, cyanobacteria appear physically less dense than corticated red algae, lacking the same hard external tissues. A lack of hard tissues could make cyanobacteria easier to mechanically process when feeding, consistent with observations of larger handling times for crustacean prey (Hoyle & Keast, 1987). Under the patch model of optimal foraging theory, a foraging strategy involving long travel to distant patches is linked with low quality of nearby patches (Charnov, 1976). A forager will leave a patch and continue searching when the rate of energy gain in a patch has been reduced below what could be obtained elsewhere (Stephens & Krebs, 1986). If cyanobacteria are particularly easy to process, then the "quality" (here related directly to quantity) of cyanobacteria patches may be reduced sooner than that of red

algae, prompting patch exit and further exploration. These differences could result in a foraging strategy with shorter patch residence times, and larger territory sizes on average (Charnov, 1976; Stephens & Krebs, 1986). Corticated algae patches on the other hand may maintain their quality long enough to favor long patch occupancy, and smaller range sizes.

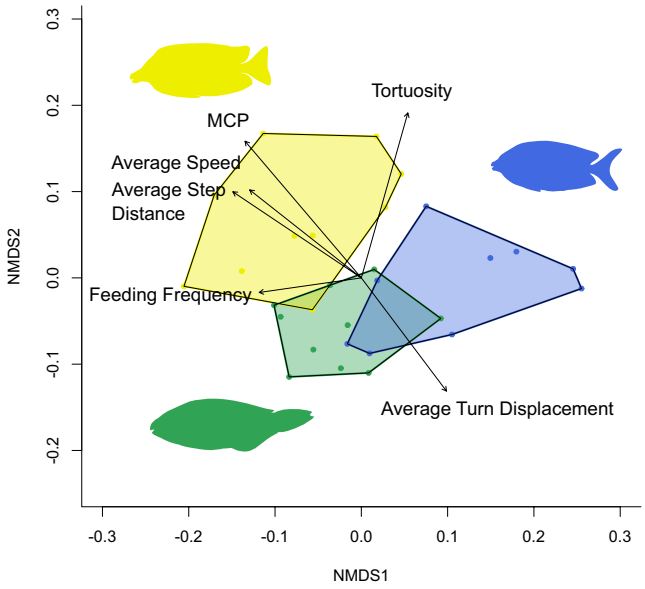

FIGURE 5 Nonmetric multidimensional scaling ordination depicting differences in foraging paths of three species: the rabbitfishes *Siganus vulpinus* (yellow), *Si. corallinus* (blue), and the parrotfish *Scarus schlegeli* (green). Convex hulls represent minimum convex polygons for all individuals of a species. Vectors represent the loadings

Another difference between these two food sources is that cyanobacteria are considered unpalatable for many species and produce metabolites to deter their consumption (Capper et al., 2006; Paul et al., 1990, 1992). Toxin constraint models predict foragers should exhibit partial food preferences, consuming multiple food types even when a toxin-producing food item is most nutritionally profitable (Stephens & Krebs, 1986). In this way profitability of food items will be balanced against toxins they contain. This balance was illustrated for reef herbivores in a study by Hay et al. (1994) where, when given a choice between a control food source and one supplemented with metabolites, reef and seagrass parrotfishes almost exclusively consumed the control food sources. Because of this, *Si. vulpinus* may need to supplement its diet with other food sources that, while less preferred, produce less toxin. For instance, dense, mat-forming species of cyanobacteria (e.g., genus *Lyngbya*) are expected to produce more toxins than their sparser counterparts (Cissell et al., 2019). Consequently, short patch residence times and wide movements for *Si. vulpinus* may be due to the quicker depletion of less-dense cyanobacteria patches that produce less toxin. However, without similar choice experiments on these species, it is unclear how much rabbitfishes are constrained by cyanobacterial metabolites.

The feeding efficiency approach given here reveals some intriguing differences between species. However, without clear info

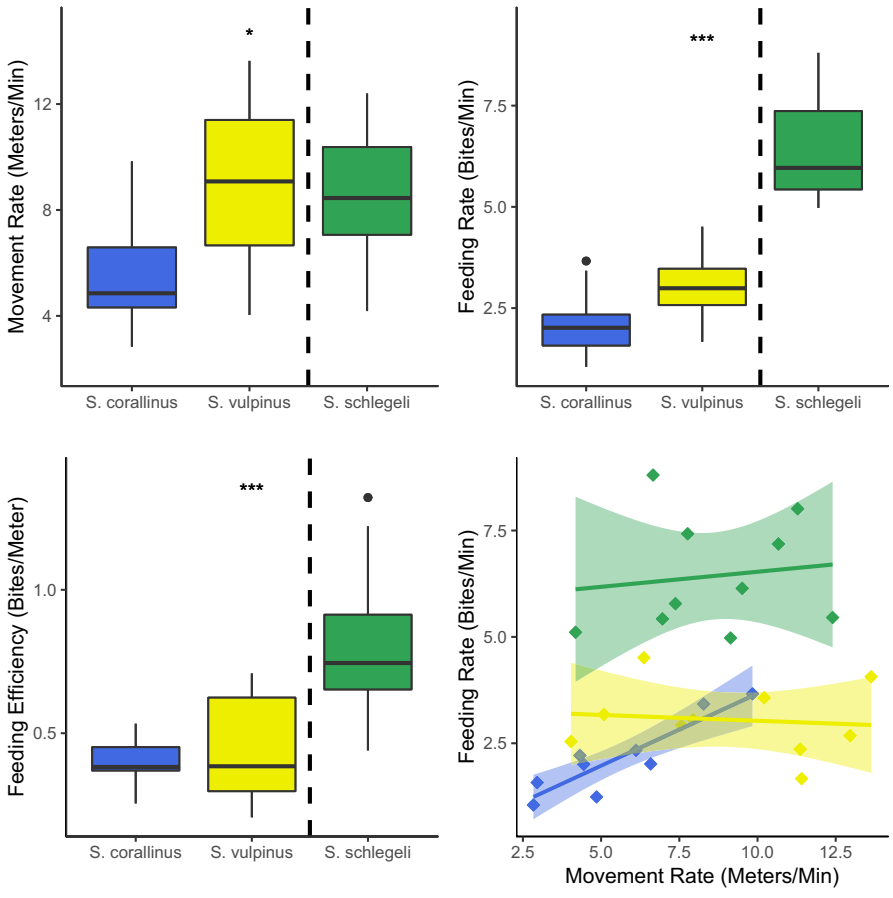

FIGURE 6 Feeding rate, movement rate, and feeding efficiency of the three species. Asterisks indicate significant differences among species via ANOVA. Boxplots represent the median and interquartile range of each foraging trait. Dashed lines separate the two grazing rabbitfishes from the scraping parrotfish

on nutritional content and assimilation efficiency these comparisons are solely exploratory. Energy budgets are complex and, in addition to these nutritional factors, are a result of other properties like body size and swimming style/speed. The two families differ substantially in their locomotion: while rabbitfishes rely largely on undulating caudal and pectoral-caudal propulsion, wrasses (such as parrotfishes) almost exclusively use flapping pectoral propulsion (Fulton, 2007). Energetic studies have suggested that flapping, pectoral propulsion (labriform swimming) is more energy efficient than undulating (Korsmeyer et al., 2002) or rowing pectoral propulsion, the latter of which rabbitfishes frequently employ for fine-scale maneuvering (Jones et al., 2007). Thus, in principle, one may expect that the parrotfish could meet energetic demands with lower feeding efficiency than the two rabbitfish species. Nevertheless, there are important other considerations that can underpin energetic demands, such as energy and nutrient content of food items. First, given the strong relationship between body mass and metabolism, a *Sc. schlegeli* of 20 cm (192 g, estimated using length-weight relationships) would have a resting metabolism approximately nearly 50% higher than than a *Si. corallinus* of equal length (117 g) and would require substantially more energy (Clarke & Johnston, 1999). Second, by scraping microbes from the calcareous reef matrix and winnowing through unwanted material, energetic and nutritional net gains per bite may be low for the parrotfish (Clements et al., 2016), thus necessitating high ration of bites per unit distance covered during foraging despite the lower energetic demands of labriform locomotion. In contrast, procurement of algae may be relatively easy for the two rabbitfishes. Our findings highlight the important need to investigate reef herbivores through an energetic and nutritional lens to fully understand the drivers and consequences of their foraging patterns.

Protecting valuable ecosystem functions requires an understanding of variations within and between functional entities (Brandl et al., 2019). Our work highlights the importance of foraging behavior as an important dimension in species management, as nuanced behavioral differences among fish species can indicate strong species-specific patterns of space and resource use that can result in complementarity in functional roles. This complementarity is ultimately driven by differences in species' energy budgets, which emphasizes the need for detailed examinations of consumer species, their food choices, and the functional consequences of this interaction.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest exist.

AUTHOR CONTRIBUTION

Robert F. Semmler: Conceptualization (equal); Formal analysis (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (equal). **Simon J. Brandl:** Conceptualization (equal); Data curation (lead); Formal analysis (equal); Methodology (equal); Supervision (equal); Writing-original draft (supporting); Writing-review & editing (equal). **Sally A. Keith:** Supervision (equal); Writing-review & editing (supporting). **David R. Bellwood:** Funding acquisition (lead); Methodology (supporting); Resources (lead); Supervision (supporting); Writing-review & editing (equal).

ETHICAL APPROVAL

All work was conducted in with accordance with JCU ethics standards on animal research, research was approved under JCU Ethics Approvals A1700 and A2086.

DATA AVAILABILITY STATEMENT

The feeding path and active tracking datasets analyzed in this study are available in the FigShare repository (https://doi.org/10.6084/m9.figshare.12233579) and (https://doi.org/10.6084/m9.figshare.12233567).

ORCID

Robert F. Semmler https://orcid.org/0000-0003-1257-5859
Simon J. Brandl https://orcid.org/0000-0002-6649-2496
Sally A. Keith https://orcid.org/0000-0002-9634-2763
David R. Bellwood https://orcid.org/0000-0001-8911-1804

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